The effect of land-use on soil organic carbon dynamics in the Peruvian Andes

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This thesis is submitted for the degree of Doctor of Philosophy at the University of St Andrews

March 2015

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~ Acknowledgments ~

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~ Abstract ~

Soil carbon storage in tropical ecosystems is important in the global carbon cycle, yet consensus is lacking on how soil organic carbon stocks are altered under anthropogenic land-use change. This thesis seeks to quantify soil carbon stocks, the associated soil carbon emissions and explores the drivers of soil respiration in managed tropical Andean lands over a 2600 m elevation gradient. It investigates: grazing and burning on high altitude montane grasslands, burning in montane forests and agriculture in premontane forests. Changes among land-uses were quantified using belowground carbon stocks, the carbon distribution among density fractions, soil carbon emissions and environmental drivers of soil respiration. Soil respiration was a good proxy of soil carbon loss in premontane pastures and montane grassland soils. The total carbon stocks on some land-uses appeared to be unaffected but the distribution of carbon within the soil had changed and even when there were no net changes in soil carbon emissions, the drivers of respiration were different. The synergistic effect of burning and grazing in montane grasslands was the most detrimental to soil carbon stocks, whereas montane forests were unaffected. In the premontane elevation, soil carbon loss was dependent on the type of agricultural practice but the succession of secondary forest allowed soil carbon to recover to similar levels measured in the mature forest.

These findings highlight the fact that although land-use does not always appear to have an obvious effect on total soil carbon stocks, the loss of carbon from short-term labile pools can cause higher carbon emissions and dominate soil-atmospheric feedbacks. Furthermore, the drivers of soil respiration and the synergistic relationship between soil moisture and temperature alter under different land uses. These factors should be taken into consideration with regards to predictions of regional temperature/precipitation climate change and soil carbon management policy in order to arrive at more realistic decisions.

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~ Chapter 1 ~

Introduction

Kosñipata valley in the tropical Peruvian Andes.

1.1 The global carbon cycle

The carbon (C) cycle is the natural biogeochemical exchange of C among four main reservoirs (atmosphere, oceans, geosphere and terrestrial ecosystems) and is fundamental in regulating atmospheric carbon dioxide (CO_2) levels and Earth's climate (Figure 1.1). The oceans, atmosphere and terrestrial ecosystems dominate a dynamic short-term cycle, transferring between 1000 and 100, 000 million metric tons of C every year, from one reservoir to another (IPCC, 2013). The C budget is the balance of C among these reservoirs.

Terrestrial ecosystems include both above (450-650 Gt C) and belowground biomass (1500 - 2400 Gt C) (Houghton, 2007; Jobbágy and Jackson, 2000). The net exchange of C between the terrestrial biosphere and atmosphere is achieved through the uptake of CO_2 by photosynthesis and release by plant respiration, soil respiration and natural disturbance (e.g. fire), which is also known as net ecosystem productivity (NEP). Total global NEP has a wide range of uncertainty and interannual variability but is the most useful summary of terrestrial activity, with net uptake estimates of ~ 10 Gt C yr^{-1} (Steffen et al., 1998). The oceans contain approximately 38,000 Gt C, where CO_2 is absorbed and chemically reacts with dissolved organic C and transported into deeper waters or is taken up by phytoplankton through photosynthesis. The ocean-atmosphere exchange of CO_2 is in equilibrium with ~ 90 Gt C transferred in each direction (Falkowski et al., 2000). The geological component typically reacts over millions of years, affecting the climate very slowly through processes such as: volcanism, sea floor spreading, weathering and dissolution and is typically not included in short term C budgets of a century (Houghton, 2007).

For the last serval thousand years, atmospheric CO_2 concentrations have remained relatively stable, with a balance between C sources and sinks. However, this finely balanced cycle is now inextricably linked to anthropogenic activities, with fossil fuel combustion, land-use activities and cement production the principal sources of CO_2 emissions to the atmosphere (IPCC, 2014). Since the beginning of industrialisation, atmospheric CO_2 concentrations have gradually risen from 277 ± 1.2 parts per million by volume (ppmv) to its present value in 2014 of 398.55 ± 0.12 ppmv (Tans and Keeling, 2014). Consequently, the release of CO_2 to the atmosphere from anthropogenic activities is too fast for the oceans and terrestrial biosphere to absorb the excess C fast enough.

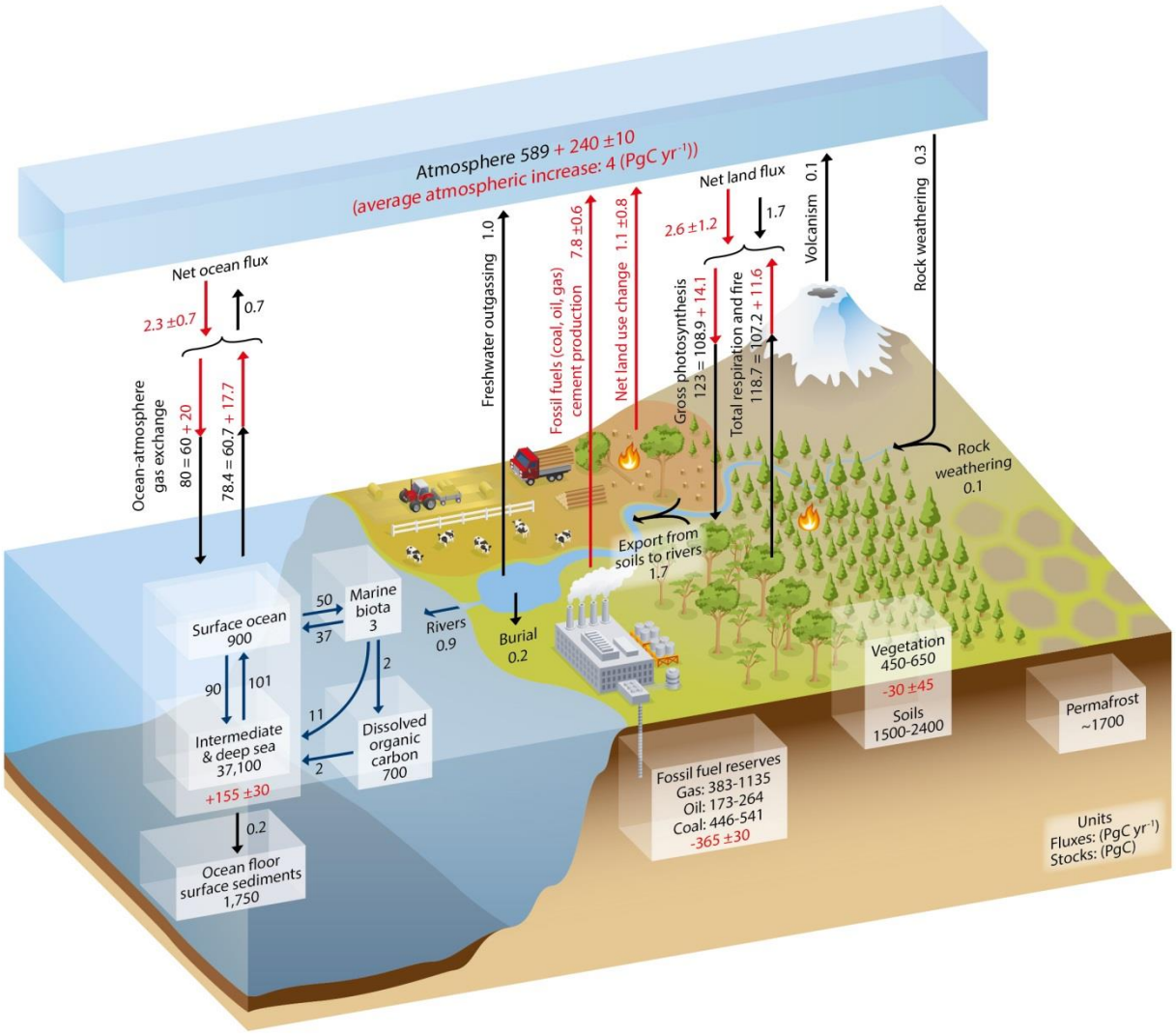


Figure 1.1 The global C cycle with focus on changes to the fast domain. The numbers represent the estimated reservoir mass ('carbon stocks') in Pg C yr^{-1} (1 Pg C = 10^{15} g C) and the magnitude of the different exchange of fluxes in Pg C yr^{-1}. Black numbers and arrows indicate reservoir mass and exchange of fluxes for the time period before the Industrial Era (1750). Red numbers and arrows indicate annual 'anthropogenic' fluxes averaged over the time period 2000-2009. This includes: net land-land use change, fossil fuel and cement emissions of CO_2 and the growth rate of CO_2 in the atmosphere. Red arrows and numbers also include cumulative changes to carbon sinks (net land flux and net ocean flux) over the Industrial Period (1750-2011), taken from (IPCC, 2013).

The resulting higher CO_2 concentrations are of concern because of an 'enhanced greenhouse effect', which increases the degree of incoming radiation trapped from the sun. Over the period from 1880 to 2012, global temperatures have increased between 0.65 to 1.06 °C and depending on future greenhouse

gas emissions, further warming over the 21st century could be anything between 0.3 - 4.8 °C (IPCC, 2014). These higher temperatures could lead to global climate changes, including more intense and frequent fires, longer periods of drought and an increase in the number of tropical storms (IPCC, 2007). Furthermore, warmer temperatures could cause faster decomposition rates of organic matter, resulting in a positive feedback between CO_2 emissions from soils and further temperature increase (Davidson and Janssens, 2006). In order to develop climate policies and project future climate changes, an accurate assessment of CO_2 emissions and C redistribution among the different C reservoirs is essential.

1.2 Uncertainties in terrestrial ecosystem C stocks

Soils have a huge capacity to store C, with estimates ranging between 1500 – 2400 Gt C (IPCC, 2014), which is almost 80 % of the total amount of C found in terrestrial ecosystems (Lal, 2004; Jobbágy and Jackson, 2000). The C stored in soils can be in both organic and inorganic forms and an important characteristic of soil is that C is stored on several timescales, therefore contributing to both short and long term C cycling. The interactions between the inorganic components of soils and atmosphere occur over very long timescales through weathering, dissolution and carbonate precipitation (Berner and Lasaga, 1983). Whereas, the main losses of organic C from soil is decomposition by soil fauna (fungi and microbial communities) into CO_2, which can occur within a few hours up to >100,000 years (Torn et al., 1997). For example, 25 % of the world's soil organic matter started to develop after the last major deglaciation (Harden et al., 1992).

Land-use activities (management of land and changes in land-use/cover), over the last century are releasing these influential long term C stores to the atmosphere, with annual net CO_2 emissions of 0.1 to 1.7 Gt C yr^{-1} during 2001 to 2011. In the last three decades, greenhouse gas emissions from land-use activities have appeared to decline by ~10 %. However, this is more a reflection of the increasing fossil fuel proportion in the last 50 years (Friedlingstein et al., 2013), rather than a significant decrease in land-use activities and land-use activities still remain the second largest source of greenhouse gas emissions (IPCC, 2014).

Historically, terrestrial C cycling research has concentrated on aboveground biomass and soil C research was focused on determining soil fertility (Trumbore, 2006). However, the important role of soil in the global C cycle and the growing demand for soil as a human resource has caused a wide and new interest in the science of soil C and in recent years there has been a surge in studies trying to improve our understanding of soil C stocks and CO_2 fluxes. In particular, the potential for C sequestration from secondary forest regrowth as a result of agricultural abandonment and the sustainable management of agricultural practices is beginning to take a forefront position in policy making on climate change mitigation (Lal, 2004).

Despite this growing body of research, global soil C stocks and CO_2 emissions from land-use change still remain the least understood component of the global C cycle (Scharlemann et al., 2014). In particular, the errors associated with estimating losses and gains of C in the tropics are three to four times higher than in temperate regions (Penman et al., 2003). This is due to many factors, such as: the extreme heterogeneity of soils, type of land use, method of clearance, land-use history, insufficient sampling depth and missing correctness for differences in bulk density (Jobbágy and Jackson, 2000). In addition to this, there is the added complication of several feedbacks linking climate, ecosystems and human activities (Jenkinson et al., 1991). For example, the fertilising effects of rising CO_2 concentrations, changing climate, nitrogen deposition, secondary regrowth of vegetation and accumulation of soil C pools after afforestation and land use changes (Le Quere et al., 2009; Cochrane and Barber, 2009; Houghton et al., 2000; Laurance and Williamson, 2001). Figure 1.2 illustrates some of the complexities in the climate-ecosystem relationship with some of the more established and theorized feedbacks in the scientific literature. The question also arises whether and how the impact of land management on soil C stocks will interact with changes in precipitation and temperature (Scharlemann et al., 2014). As a result, the uncertainties surrounding the impact of soil C stocks with land management and the magnitude of long-term soil CO_2 fluxes need to be further quantified (Davidson and Janssens, 2006; Reichstein et al., 2005b).

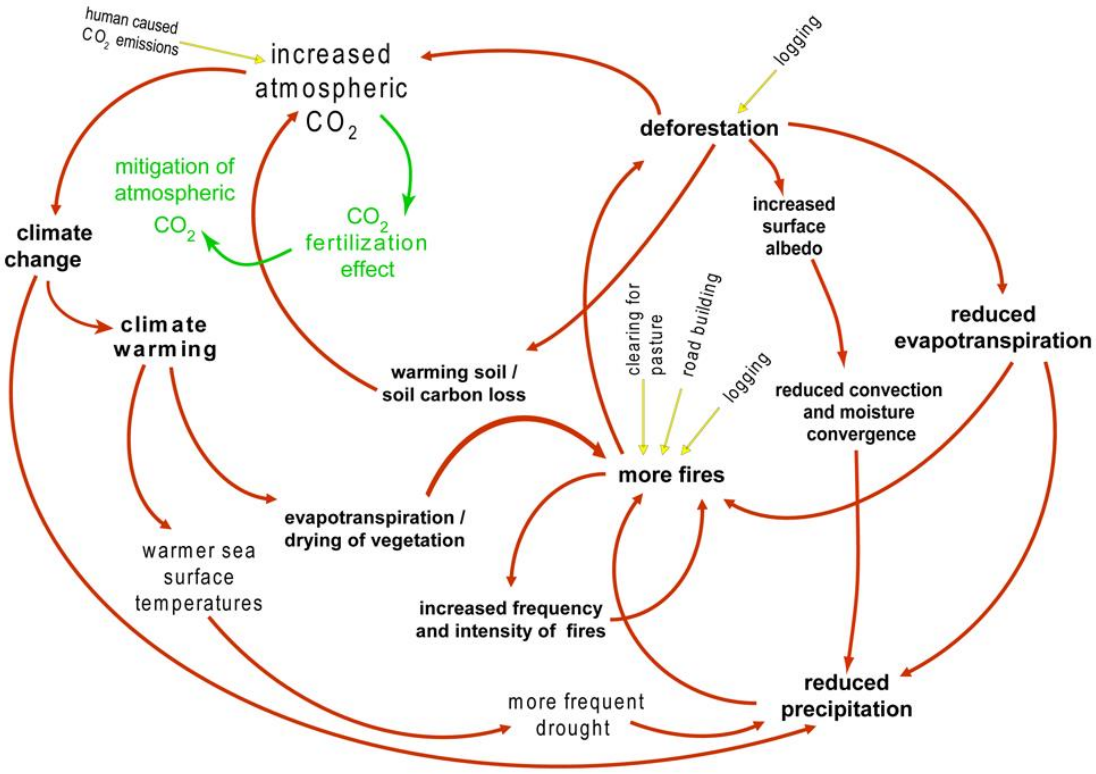


Figure 1.2 Schematic representation of the climate-ecosystem relationship, illustrating some of the many established and theorized feedbacks in the scientific literature (UNEP, 2011).

1.3 The nature of soil organic matter and drivers of soil respiration

In order to identify the extent of soil C loss or the C sequestration potential of soil in relation to land-use change, it is essential to understand how land-use activities disrupt or maintain a soil's capacity to physically protect C. Soil organic carbon (SOC) is a direct measure of the amount of soil organic matter (SOM) contained in soil and the quantity of SOC in any given soil is a balance between the rates of organic C input (vegetation, roots) and the subsequent loss of CO_2 to the atmosphere by microbial decomposition. The resulting soil matrix is made up of a continuum of materials at varying stages of decomposition with differing residence times and locations within the soil (Jastrow et al., 1998; Luo, 2006). Specifically, there are three biologically significant and measureable components (pools) that

differ in their residence time, chemistry and origin: the active, intermediate, and passive pool. The active pool has a relatively fast turnover of < 10 years, includes labile organic fragments of fresh plant material (typically >53 µm), and is typically respired back to the atmosphere. The slow or intermediate pool turns over on a decadal time scale and differs in size and chemistry to the active pool. The longer turnover time is explained by a proportion of this humified material being protected within soil aggregates or adsorbed on reactive surfaces of mineral particles, making it oxygen deficient and spatially inaccessible for rapid decomposition (Golchin et al., 1994a; Six et al., 2004). Finally, there is the passive pool with a turnover of centuries to millennia (Townsend et al., 1995; Christensen, 2001). The persistence of this material is partly a consequence of the type of plant material, its biochemical recalcitrance and accessibility to decomposers (Six and Jastrow, 2002) (Figure 1.3).

The rate at which SOM decomposes is dependent on many factors, but the principal controllers are the quantity and quality of the material entering the soil; the proportion of sand, silt and clay making up the soil, which will in turn influence how physically protected the SOM is within the soil; and external environmental factors, such as: temperature and moisture (Bosatta and Ågren, 1999; Ise and Moorcroft, 2006; Trumbore, 2006; Kutsch et al., 2001). Temperature can directly affect decomposition by promoting microbial activity and/or indirectly by altering soil moisture and the quantity and quality of organic matter input to the soil (Chapin III et al., 2011). An exponential increase in the rate of mineralisation of C to CO_2 can generally be seen over a broad range of temperatures (Figure 1.4), with many microbial communities acclimatising to higher temperatures. In the tropics, the continuously high temperatures in the tropics can explain why these ecosystems have such a small litter pool despite their high productivity. High and low soil moisture, on the other hand, causes greater restrictions on decomposition, with decomposers at their most productive when oxygen is sufficiently available (Gholz et al., 2000) (Figure 1.5).

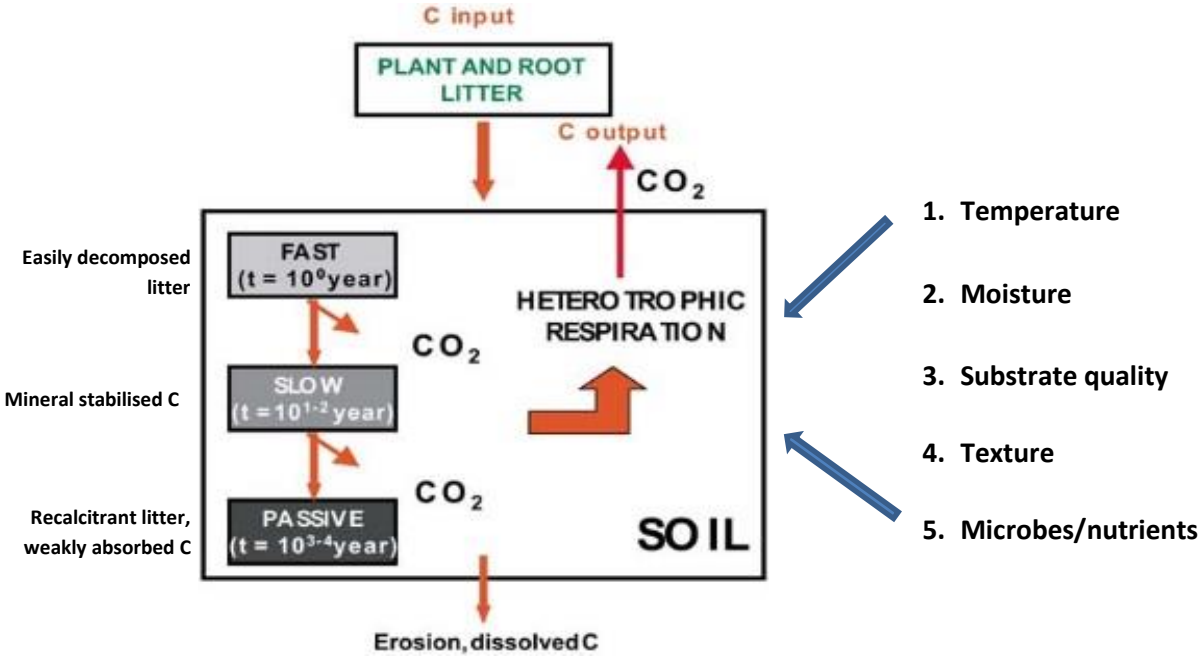


Figure 1.3 Simplified schematic of soil carbon balance and the main controlling factors influencing soil organic matter decomposition (adapted from (FAO, 2004)).

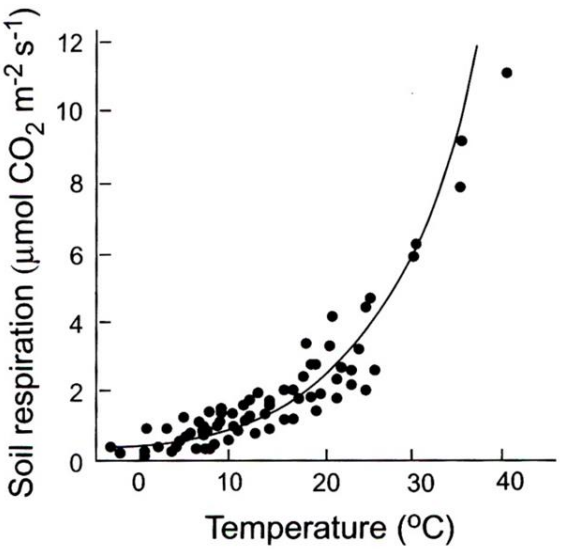


Figure 1.4 Relationship between temperature and soil respiration in field measurements of soil respiration in 15 studies. Redrawn by (Chapin III et al., 2011) with permission from (Lloyd and Taylor, 1994).

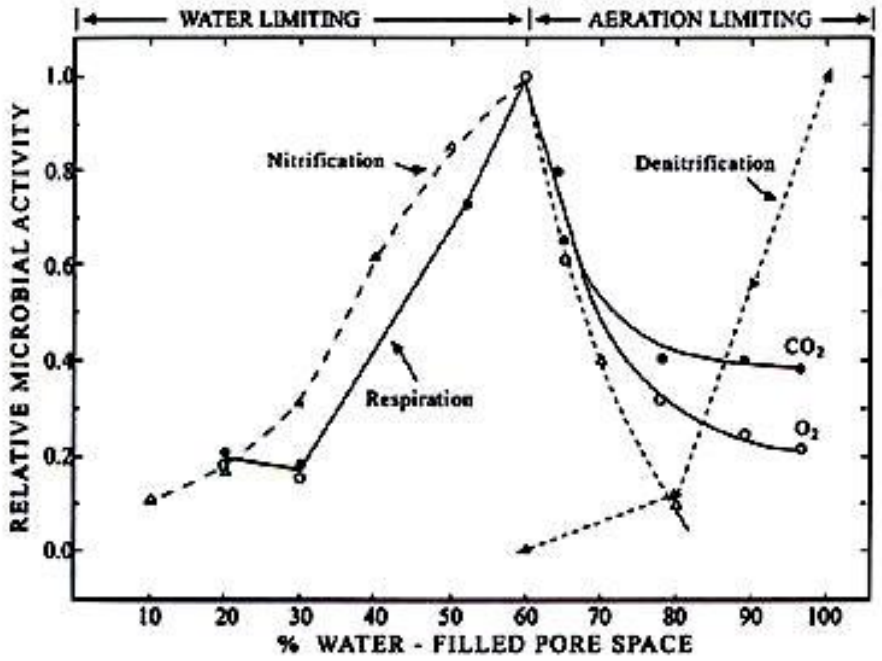


Figure 1.5 Influence of water-filled pore space on microbial activity (Cleemput and Boeckx, 2005).

1.4 Alterations to SOC stocks with land-use change

The predominant reasons for changes in the decomposition rates of SOC under differences land-uses are: (i) due to changes in microclimate; (ii) alterations in the quantity and quality of C cycled through the system and (iii) soil structural changes (Raich and Tufekciogul, 2000; Davidson et al., 2000a).

After land cover changes, the microclimate of the soil can be altered, especially when there is a more open canopy or when changes in bulk density increase water logging. Studies have shown that in humid regions, soils may be more vulnerable to land-use change than dryer regions because the impact of precipitation can be greater (Lugo and Brown, 1992; Don et al., 2011). The main uncertainties are how land-use affects the relationship between soil moisture and temperature with soil respiration and whether there are any synergistic effect of these two drivers (Craine and Gelderman, 2011). Also, SOC is directly associated with soil parameters such as clay content as they provide mineral surfaces for the physical protection and stabilization of SOC (Feller and Beare, 1997). However, despite the importance of

measuring these soil attributes, only 25 % of studies have measured them, leading to over estimations of C losses (Don et al., 2011).

When considering the short and long term storage effects of SOC with land-use change, the importance of measuring the different C pools, as well as the bulk soil C content, have been highlighted in many tropical, temperate and boreal studies (Marin-Spiotta et al., 2009). For example, the active pool may only be small but its fast turnover rates of C can dominate atmospheric feedback interactions (Silver et al., 2000; Bayer et al., 2001), whereas, long term effects may be observed in the slower pools and characterised by the soil's ability to physically protect C (Six et al., 2002a). Uncertainties lie in how sensitive these fractions are to land-use change. In most studies, the labile pool is said to be the most sensitive to vegetation changes and directly linked to soil CO_2 emissions (Wang and Wang, 2011; Conant et al., 2011; Franzluebbers and Stuedemann, 2002). In comparison, the effect on the stabilisation of SOM in the passive pools are less well known.

After conversion of forest to agricultural land, the immediate loss of C is substantial and a major proportion of the total SOC change occurs during the first few years (usually from the loss of labile C). However, these systems eventually reach a new equilibrium once the processes involved in the decomposition of organic matter are stabilised (Post et al., 1982; Batjes, 1997). This re-establishment of a new equilibrium or steady state can take anything from 3-10 years (Detwiler, 1986) and even up to 50 years in some systems (Baldock and Skjemstad, 2000; Poeplau and Don, 2013). In an apparent equilibrium, the total SOC content of the soil is based on the balance between the gradual build-up of new material (e.g. from grasses) and the decay of the original forest C.

In addition to measuring how C is distributed within the soil matrix, stable natural abundance isotopes can be used to determine the origin of C, giving useful insight into the turnover rate of organic matter (Marín-Spiotta et al., 2008). Stable natural abundance isotope techniques are useful when tropical forests are converted into grassland because of the different photosynthetic pathways between C3 (trees) and C4 (grasses) plants, which use naturally abundant ^{13}C isotopes to different degrees. As a result, significantly different isotopic signatures occur, with tropical trees being relatively depleted in $\delta^{13}C$ (-12 to -30 ‰) and

grasses more enriched in $\delta^{13}C$ (-10 to -15 ‰) (Ehleringer et al., 2000). This then makes it possible to distinguish new C input into the soil from original vegetation from those of recent vegetation (Lemma et al., 2006). The relative contributions of C3 trees and C4 grasses to the soil organic matter can then be quantified using a mass balance (Marin-Spiotta et al., 2009).

1.5 SOC stocks and current rates of land-use change in the tropics

Tropical soils play a particularly critical role in regulating atmospheric CO_2 concentrations, containing approximately a third of global soil C (Jobbágy and Jackson, 2000) (Figure 1.6). Before about 1950, C emissions from land-use change were mainly from temperate regions. In recent decades, however, C releases from land-use change have been concentrated in the tropics (Achard et al., 2014), with approximately 7.6 million hectares of tropical forest deforested in the 2000s (Achard et al., 2014), leading to a 7.7 % loss in soil C (Scharlemann et al., 2014). As a result, land-use change in the tropics now accounts for 12-20 % of all anthropogenic induced greenhouse gasses (IPCC, 2014; Werf et al., 2009).

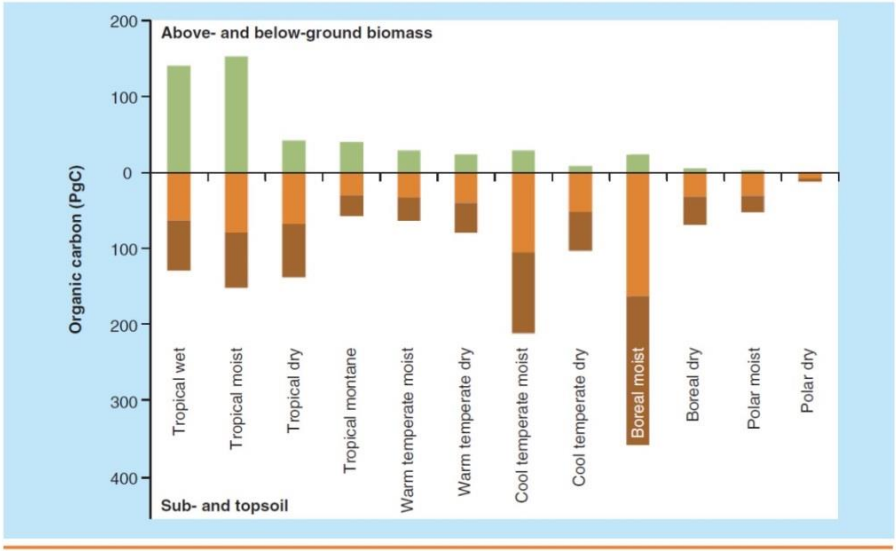


Figure 1.6 Global distribution of organic carbon stocks in sub- (dark brown) and topsoil (orange) from (Hiederer and Köchy, 2011), and in above- and below-ground phytomass (green) from Ruesch and Gibba by IPCC climatic regions, taken from (Scharlemann et al., 2014).

Although deforestation rates in the tropics are slowing down, South America still has one of the highest deforestation rates, globally (FAO., 2010) (Figure 1.7). The dominant land-use changes are conversion of primary forest to agricultural practices (Li et al., 2005; Pinto et al., 2006; Trumbore et al., 1995; Davidson et al., 2000a; Salimon and Davidson, 2008; Salimon et al., 2004), which account for 80 % of the deforestation (Kissinger and Herold, 2012).

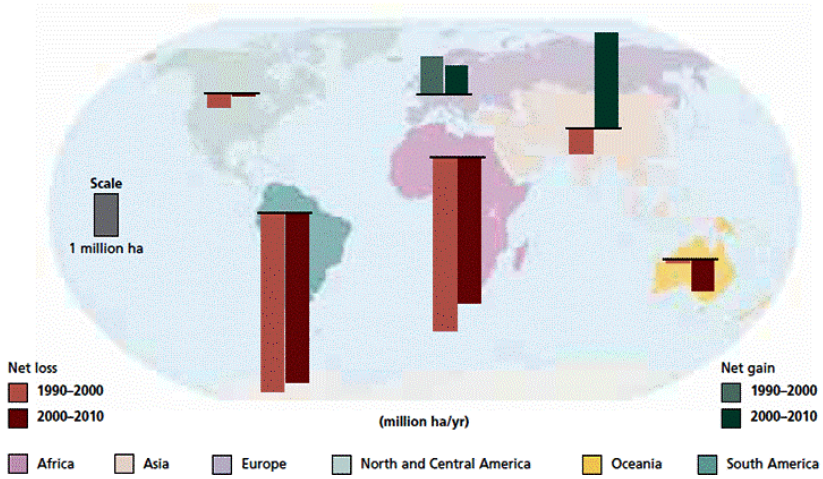


Figure 1.7 Annual change in forest by region between 1990-2010, taken from (FAO., 2010)

1.6 Case study: Tropical Andes

1.6.1 Land-use change in the Peruvian Tropical Andes

Peru has the third largest tropical forest in the world, covering 661 000 km^2. However, these forests are increasingly under threat from anthropogenic land use changes, with estimates in 2005 of 545 km^2 yr^{-1} of forest lost or disturbed (Oliveira et al., 2007). In particular, activities such as burning and grazing are taking place in the high elevation zones and the increasing demands for agricultural produce are causing massive areas of deforestation in the lower elevations. There is also an abundance of secondary forests from the abandonment of farms and selective logging (Figure 1.8) (Aide and Grau, 2004; Lambin and Meyfroidt, 2011). Yet despite the acknowledged importance for soil C storage in the Peruvian tropical Andes (Zimmermann et al., 2009c; Girardin et al., 2010) and threat from anthropogenic intervention, we have relatively few ground-based measurements of soil respiration on different land uses and know relatively little about how this affects soil C stocks in this region. Many of the tropical land use change studies have taken place in Brazil, Malaysia and Puerto Rico (Fearnside and Imbrozio Barbosa, 1998; Melling et al., 2005; Wick and Tiessen, 2008; Guimarães et al., 2013; Doff Sotta et al., 2004). This study was based in the south-eastern tropical Andes in the Manu Biosphere Reserve, which spans 1.5 million hectares and covers successive tiers of vegetation rising from 150 to 4200 m a.s.l. The ecosystems investigated ranged from high elevation montane grasslands (3200 m a.s.l), upper montane forest (2200 - 3200 m a.s.l) down to premontane forest (500 - 1200 m a.s.l) (Table 1.1). Despite the protection of these forests, they are not carefully managed and anthropogenic activities still take place. A unique aspect to this study is that by encompassing the three elevation bands, it gives a good depiction of the many land management activities occurring in the Andes and how soil C storage is affected in the different ecosystems and under different climates. Figure 1.9 illustrates the expansion of high elevation grasslands

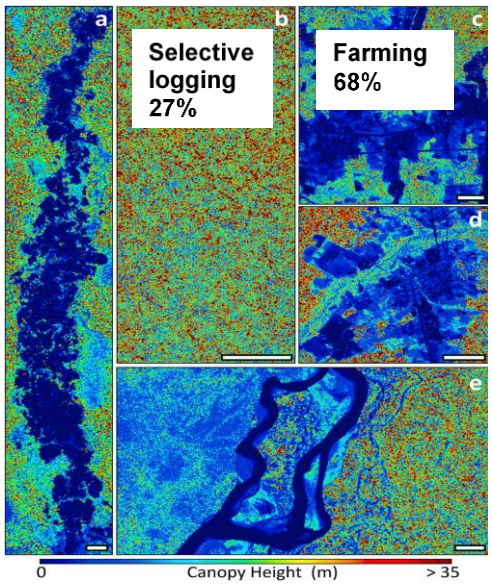


Figure 1.8 Sources of variation in forest canopy height detected with high-resolution Carnegie Airborne Observatory LiDAR in the Peruvian Amazon between 1999 and 2005 (Asner et al., 2010).

into the montane cloud forest as a result of burning activities and an aerial photograph of the premontane area studied. Further details of the sites chosen at each elevation are given in chapter 2.

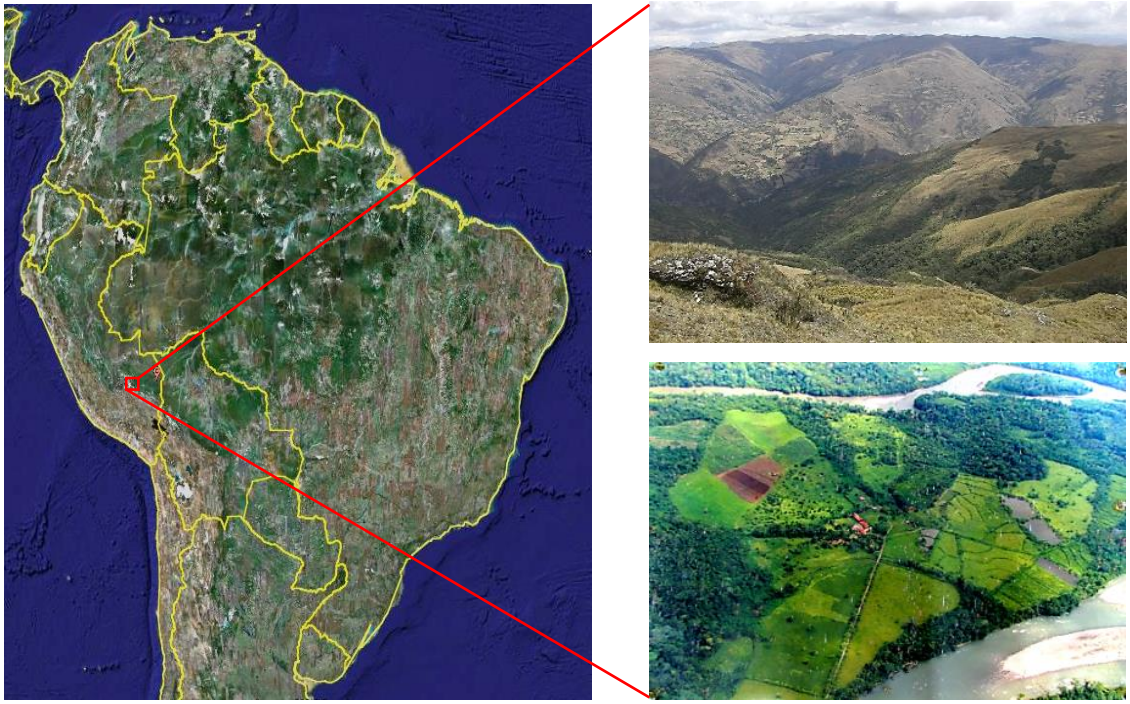


Figure 1.9 Map of South America and the region studied in Peru is highlighted in red. Aerial photographs of the premontane area (bottom right) and montane grassland and montane forest (upper right).

Table 1.1 Background information on the three elevations chosen in this study taken from (Zimmermann et al., 2009c; Girardin et al., 2010; Oliveras et al., 2013; Román-Cuesta et al., 2011).

Ecosystem	**Dominant vegetation**	**Elevation (m a.s.l)**	**Annual precipitation (mm)**	**Mean Temperature (° C)**	**Typical land use management**
Montane grassland	*Calamagrostis longearistata; Scirpus rigidus; Festuca; dolichophylla;*	3121	1560	11.8	Burning for cattle grazing
Montane cloud forest	*Weinmannia crassifolia; Clusia flaviflora; Clusia alata*	3025	1710	12.5	Burning on the tree line as a result of increased fires in the montane grassland
Premontane rainforest	*Precatoria; Guaduinae*	580	4500	22	Agricultural practices (e.g. Banana plantation, cattle grazing, pineapple, guava, rice, coffee)

1.6.2 Changes in climate in the Peruvian Tropical Andes

Under even the more conservative climate change scenarios, the tropics are expected to experience climate changes one decade earlier than the global average (Mora et al., 2013). In particular, high elevation tropical mountain regions are predicted to be more strongly affected by climate changes than their surrounding lowlands. This is of major concern because of how changes to the climate will affect socio economic activities as well as Andean ecosystems and downstream water supply (Vuille et al., 2003). The relatively small natural climate variability and narrow tolerance to large fluctuations in temperature in these ecosystems means that even the smallest temperature change can cause wide spread extinction of many species. This is especially the case if the given changes occur quickly, not allowing for species to acclimatise.

Climate modelling in the Andean tropical mountain range is particularly challenging because of its complex topography and steep climatic gradients (Urrutia and Vuille, 2009). However, even under optimistic climate change scenarios, predictions of significant warming in the tropical Andes have been made with ~ 5°C warming by the end of the 21st Century and an increase in interannual temperature variability (IPCC, 2014). As global mean surface temperature increases, precipitation events are also expected to be more extreme and dry-seasons more intense. In South America, predictions have been made of a ~2 mm day^{-1} increase in precipitation between December to May and ~1 mm day^{-1} for June to November, with evaporation increases of 0.2 – 0.6 mm day^{-1} for the whole year (Kitoh et al., 2011). Similar predictions have been made across the Andes with ~1-2 mm day^{-1} in precipitation and slightly more in the wet season than dry (Urrutia and Vuille, 2009; Vera et al., 2006). However, the largest uncertainties of future estimates of regional climate change lie in what the future greenhouse gas emissions will be depending on mitigation efforts (IPCC, 2014).

Figures 1.10 and 1.11 illustrate past and future predictions of temperature and precipitation for the tropical montane cloud forest and premontane rainforest sites chosen for this study. The four possible scenarios, known as representative concentration pathways (RCPs) are based on the most recent IPCC AR5 report (IPCC, 2014); (taken from http://climexp.knmi.nl/help/atlas_scenario.shtml):

- RCP8.5 is a business-as-usual scenario with increasing greenhouse gas emissions over time, leading to high greenhouse gas concentration levels,
- RCP6.0 is a stabilization scenario in which emissions rise quickly up to 2060 and then decrease,
- RCP4.5 assumes quicker action to limit greenhouse gas emissions with emissions peaking in 2040 and declining strongly until 2080,
- RCP2.6 describes an all-out effort to limit global warming to below 2°C with emissions decreasing sharply after 2020 and zero from 2080 onward.

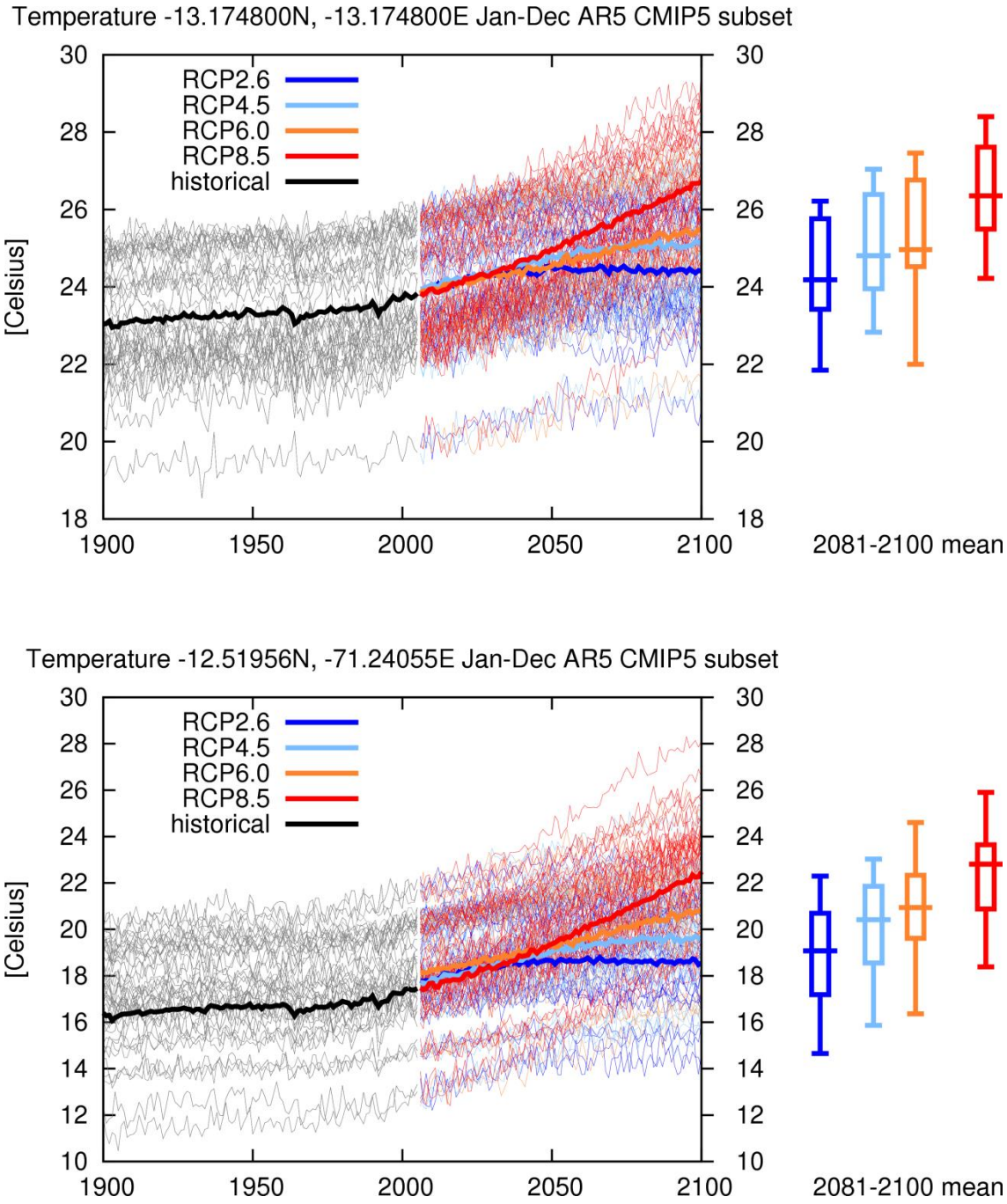


Figure 1.10 Predicted temperatures under scenario Jan- Dec AR5 CMIP5 subset for a) montane cloud forest at Wayqecha and b) premontane rainforest at Villa Carmen. On the left, for each scenario one line per model is shown plus the multi-model mean, on the right percentiles of the whole dataset: the box extends from 25% to 75%, the whiskers from 5% to 95% and the horizontal line denotes the median (50%).

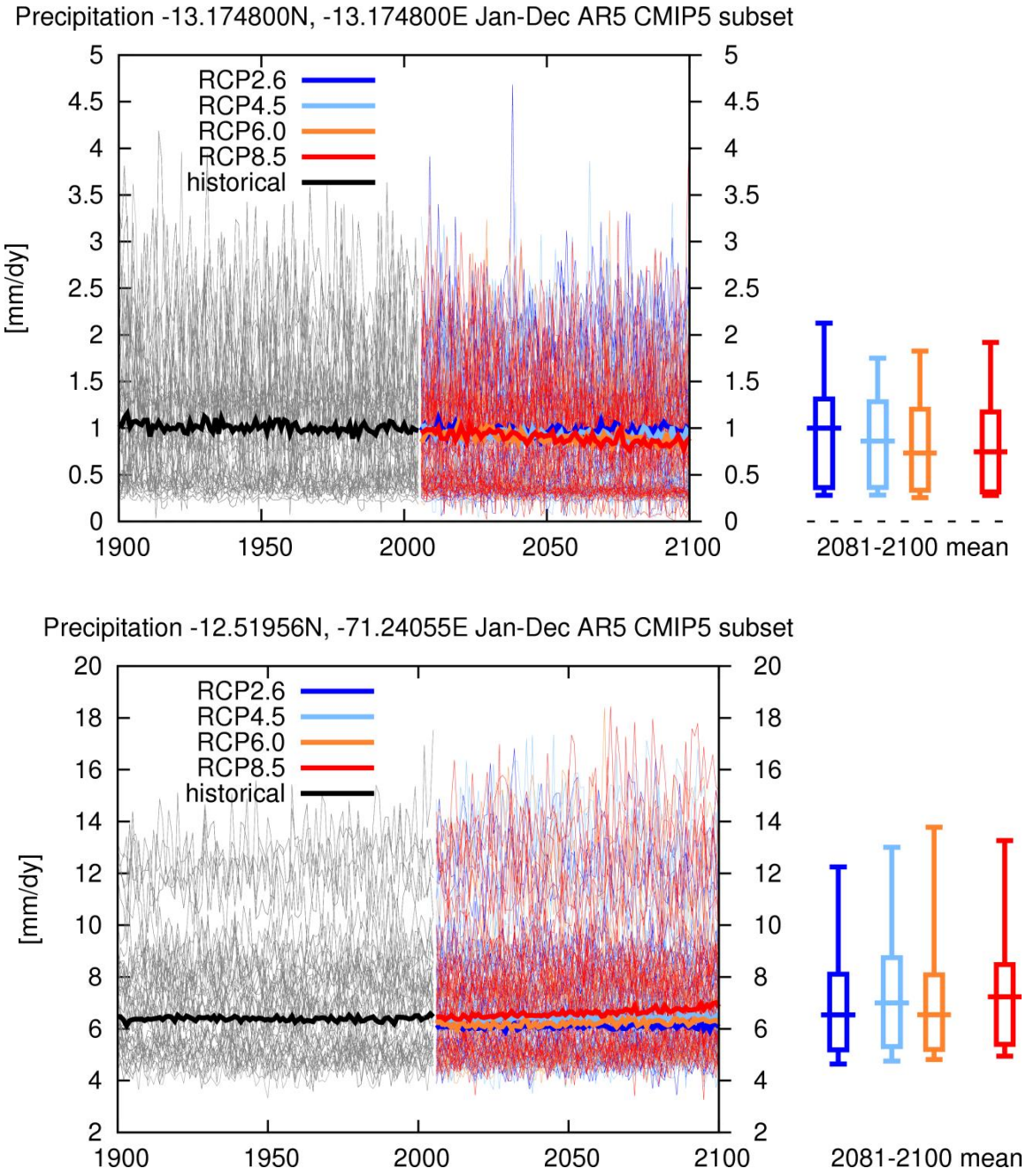


Figure 1.11 Predicted precipitation under scenario Jan- Dec AR5 CMIP5 subset for a) montane cloud forest at Wayqecha and b) premontane rainforest at Villa Carmen. On the left, for each scenario one line per model is shown plus the multi-model mean, on the right percentiles of the whole dataset: the box extends from 25% to 75%, the whiskers from 5% to 95% and the horizontal line denotes the median (50%).

1.7 Overview of the thesis

The overall aim of this thesis is to improve our understanding of the changes in soil C storage associated with managed upland tropical ecosystems. To address this aim, a combination of in-situ field measurements and laboratory manipulation experiments were undertaken. The field sites consist of a representative number of land uses and land management techniques along a 2600 m altitude gradient in the Peruvian Andes, ranging from premontane rainforest to upland grassland. The thesis is composed of three independent research chapters and a concluding chapter, providing synthesises and discussion on the implications of the findings and suggestions for future research.

The goal of the thesis is to answer the following questions:

1) Does soil C storage alter under different land uses?
2) What are the CO_2 emissions associated with land use?
3) Do the drivers of soil organic matter decomposition alter under different land uses?

Chapter 2: Turnover and storage of soil organic carbon from different land uses on an elevation gradient in the Peruvian Andes

This chapter aims to explore how soil C storage is affected by land use. This study uses a density fractionation technique to determine whether the distribution of C within the soil is different among land uses and employs a natural abundance isotope technique to estimate the turnover of C on pasture soils.

Research objectives in chapter 2:

1. Quantify and compare total SOC stocks at four depths (0-5, 5-10, 10-20, 20-30 cm) among different land uses from three elevation bands;
2. Evaluate the effect of different management systems on the labile and stable organic matter pools.

Chapter 3: Soil CO_2 flux from different land uses on an elevation gradient in the Peruvian Andes

The principal goal of this chapter is to evaluate the importance of land use change on soil CO_2 emissions and to address uncertainties in how the key environmental drivers of soil CO_2 emission are altered with land use.

Key research objectives in chapter 3:

1. Quantify differences in soil respiration among different land uses from three elevation bands;
2. Evaluate the role of environmental drivers among these land uses in regulating soil respiration fluxes, including factors such as: soil temperature, moisture, C content, texture, bulk density and rainfall events.

Chapter 4: Sensitivity of soil respiration to land-use and the combined influence of soil temperature and moisture in agricultural soils from the tropics

This chapter aims to determine the combined influence of soil moisture and temperature on heterotrophic respiration from soils with different land use histories using a short-term incubation study in a factorial experimental design. Laboratory incubations provide a controlled environment where variables on decomposition can be studied independently of confounding factors from in field experiments. Based on the findings from chapter 3, a subsample of sites was chosen to further investigate how the relationship between these two environmental drivers of soil respiration changes with land use. The temperature and moisture treatments were chosen according to the maximum and minimum values reported from the field data in chapter 3.

Research objectives in chapter 4:

1. To determine the response of heterotrophic respiration from soils with different land uses to systematic variations in soil temperature;
2. To determine the response of heterotrophic respiration from soils with different land uses to systematic variations in soil moisture;
3. To establish whether altered soil moisture content would modify the temperature sensitivity of heterotrophic respiration among soils from differing land uses.

~ Chapter 2 ~

Turnover and storage of soil organic carbon from different land uses on an elevation gradient in the Peruvian Andes

Tropical montane grasslands ‘Puna’ in the Peruvian Andes. Photograph by Sam Jones.

2.1 Abstract

Tropical soils account for a third of global soil C and play a critical role in regulating atmospheric CO_2 concentrations. The continuing fast rates of deforestation in the tropics for agricultural expansion and subsequent abandonment of new land uses are of particular interest to the science of soil C because of the associated C losses and potential for C sequestration. This study seeks to improve understanding of soil C stock changes within managed land in different ecosystems over a 2600 m gradient in the south-eastern Peruvian Andes. Using a density fractionation technique and natural abundance isotopes, the effects of the diverse range of local land use changes on 23 sites were investigated: grazing and burning on high altitude montane grasslands; burning in montane cloud forests; agricultural practices (cultivated and abandoned banana plantations, pastures of different grazing intensity), selective logging and secondary forest succession in the premontane forests. Overall, the montane grasslands and montane cloud forest had very similar soil C stocks down to 30 cm (167 ± 12 and 162 ± 36 Mg C ha^{-1}); with the premontane forest containing approximately 63 % less soil C (61 ± 2.5 Mg C ha^{-1}). The majority of the soil C pool (75 %) was recovered in the mineral - associated density fraction, with the montane grasslands containing on average ~ 10 % less C in this fraction than the premontane soils. Burning and grazing in the montane grasslands had no significant influence on the total C stocks but the distribution of physical density fractions were altered, with significantly lower labile fractions (LF) and burning alone causing higher occluded labile fractions (oLF). Burning in the upper montane forest had no significant effect on soil C stocks, except on one of the sites, which may have been a result of burning intensity or site-specific micro climate differences. Agricultural practices in the premontane elevation showed variable results in both total soil C and its distribution within the soil. Pineapple plantations had no effect on total soil C but significant losses in the LF. Cultivated banana soils had significant total C losses (16.3 ± 0.5 Mg C ha^{-1}), with the majority coming from the stable heavy fraction (HF). The recovery of soil C was notable on an abandoned banana plantation of eight years due to the input of more recalcitrant material with forest regrowth and the same was found with the secondary forest. The isotope data showed that the total soil C stocks in the pasture soils were directly linked to the proportion of forest and grass derived C in the soil, with pasture sites containing the most forest derived C showing similar total C stocks to the mature forest. This study shows that the ability of the soils to maintain SOC stocks during land use changes are largely impacted by the physical distribution of C in the soil, the origin of C and dependent on type of land use.

2.2 Introduction

Soil is one of the Earth's largest and longest terrestrial carbon (C) reserves, containing almost three times more C than all living matter found in terrestrial ecosystems and two times more C than the atmosphere (Post et al., 1990; Prentice, 2001). Estimates indicate that C emissions due to tropical land use change are 2.82 ± 0.45 Mt C per year (Pan et al., 2011), with tropical forest conversion to cropland being one of the main contributors (Don et al., 2011).

High altitudinal montane grassland (3200 - 4500 m a.s.l) and premontane forest (500 - 1200 m a.s.l) account for a major proportion of land cover in the Andes, particularly in Peru, where they make-up approximately 25 % and 22 % of land cover respectively (Feeley and Silman, 2010). Since the early 1500's, the main driving force for the expansion of montane grasslands and subsequent destruction of tropical montane cloud forest has been burning and cattle grazing (Luteyn, 1992; Cochrane and Ryan, 2009). In contrast, the premontane forests remained relatively undisturbed until the late 1990's and early 2000's (Buckingham and Shanee, 2009) when the proliferation of road construction and increased demand for agricultural exports caused mass migrations of people and high rates of deforestation (Valdivia, 2014). Specifically, between 1999 and 2000, 68 % of forest loss has been for agriculture and 27 % for selective logging (Asner et al., 2010). Conversely, there has also been an increase in successional forests (Wright, 2005) due to the low productivity of montane soils and unsustainable farming methods causing widespread agricultural abandonment (Aide and Grau, 2004; Lambin and Meyfroidt, 2011). As a result of all these activities, the Andean montane forests have become a patchwork of different land uses. Yet despite the acknowledged importance of land use change in altering soil C stocks (Post and Kwon, 2000), we still know very little about the impacts of anthropogenic intervention on soil C storage in tropical Andean ecosystems. Previous research in these systems has measured large C stores in these soils, particularly in the montane cloud forest and montane grasslands (Zimmermann et al., 2009c; Girardin et al., 2010) and the loss of C from land management could potentially be an unaccounted source of regional CO_2 (Román-Cuesta et al., 2011).

The organic C found in soils is primarily in the form of soil organic matter (SOM), which is a complex and dynamic composite of organic compounds from progressively decayed plant, animal and microbial

material in the soil matrix (Zimmermann et al., 2010a). The turnover of SOM is a balance between the inputs of material into the soil (e.g., above and belowground litter, dissolved organic C) and the rate of SOM decomposition. This rate is partly a consequence of the type of plant material and its susceptibility to degradation (biochemical recalcitrance) and the accessibility of SOM to decomposers (Six and Jastrow, 2002); the latter including adsorption of SOM to reactive surfaces of mineral particles and the physical protection within aggregates. The rate of SOM decomposition is also influenced by soil microbial communities, nutrients, dissolved organic carbon and external environmental factors, such as: soil moisture and temperature (Kirschbaum, 1995; Raich and Schlesinger, 1992).

After conversion from primary forest to agricultural land, the partial or total removal of forest cover and the reduction of litter inputs to the soil can leave the soil more exposed to intensive weather conditions, increasing potential erosion rates and influencing the micro-climatic condition within and just above the soil. In addition, the rate and type of organic matter input to the soil changes under different lands uses, thereby affecting the decomposition rates and the total C content of the soil (Tan et al., 2007). The rate and direction of soil C with land use change has been a highly researched topic because of the associated concern with greenhouse gases. The general consensus is that forest conversion for agricultural purposes causes a net loss in soil C (Guo and Gifford, 2002; Schlesinger, 1986). However, converting to pasture does not necessarily always lead to a decline in some grassland systems and have nearly the equivalent potential to store C as forest soils (Post and Kwon, 2000; Franzluebbers et al., 2000) because of their fast turnover rates. In addition, secondary forests are known for their C sequestration potential (Rhoades et al., 2000; Hughes et al., 1999) but due to an array of many different factors (e.g. land use type, intensity, time since land-cover conversion, soil properties, climate etc.), the magnitude of soil C losses or gains are inconclusive.

The heterogeneous nature of soil can disguise changes in how C is stored within the soil, leading to ambiguous conclusions that the soil C stocks have not responded to land-use changes (Bashkin and Binkley, 1998). Soil is often conceptualised in models as containing three or more different SOM pools of varying chemical properties and residence times (Trumbore, 1993; Six et al., 2002b; Bol et al., 2009). These include: labile pools with a turnover time of 1 to 5 years, which include easily available dead plant

material as a C source for microorganisms; intermediate pools turning over on decadal time scales, which contain physically and chemically transformed material residing on and within the surface of clay and silt minerals; and more stable pools with a turnover time of centuries to millennia due to the nature of the biochemically recalcitrant and bio-actively unavailable material. Even when land use change does not appear to affect the bulk soil C, the distribution of these pools may change due to their differing sensitivities (Zimmermann et al., 2007).

Labile fractions are accepted as being the most sensitive to changes in vegetation management (Cambardella and Elliott, 1993; Baisden et al., 2002; Guggenberger and Zech, 1999; Helfrich et al., 2006). Although they make up only a small part of the total C pool, they may dominate soil-atmospheric feedbacks because of large CO_2 fluxes into and out of this pool, coupled with high turnover rates (Bayer et al., 2001). However, while several studies have found the labile fraction to be more sensitive to vegetation change (Wang and Wang, 2011; Conant et al., 2011; Franzluebbers and Stuedemann, 2002), others have found no discernible effect of land use change on this pool (Leifeld and Kögel-Knabner, 2005). For instance, after land-use change from forest to pasture, some investigations have found labile fractions to decrease (Poeplau and Don, 2013), while other study sites report an increase (Cambardella and Elliott, 1993), depending on the magnitude of C inputs (e.g. roots, litter fall) or the level of grazing intensity (Figueiredo et al., 2010). On the other hand, slower pools may be a useful indicator of the long-term effects of C storage in soil because of their stabilising effect on soil C, causing a resistant effect on the total soil C (Six and Jastrow, 2002; Marìn-Spiotta et al., 2008).

Methods such as density fractionation have been routinely used as a way to physically separate SOM into fractions of varying reactivity and chemical recalcitrance and when combined with the use of natural abundance stable isotopes, they have been very successful at assessing the short and long-term dynamics of soil C storage, particularly in systems where large isotopic differences exist among C pools or inputs (Golchin et al., 1994b; Christensen, 2001). Natural abundance $\delta^{13}C$ techniques are dependent on the natural, systematic variations in the $\delta^{13}C$ composition of different C substrates to evaluate the impacts of land-use or environmental change on the reactivity and turnover of different SOM pools. Natural

abundance $\delta^{13}C$ techniques have been particularly effective in agricultural systems where transitions from C3 to C4 vegetation have occurred, or vice versa.

Despite the concern on the effects of land management practices, there are very few studies on soil C stocks in this tropical region of the Peruvian Andes, yet with increased access and demand for agricultural exports, it is important to understand how these ecosystems will respond to future management. It is particularly unclear how land management affects the soil C dynamics and sequestration potential on abandoned agricultural land. In this study, a combination of density and particle-size fractionation and natural abundance stable isotope analysis were used to gain further mechanistic insights into the impact of land-use management on different SOM fractions. A representative number of different land uses were used on a broad scale elevation gradient to investigate the following objectives:

1. Quantify and compare total SOC stocks at four depths (0-5, 5-10, 10-20, 20-30 cm) among different land uses from three elevation bands;
2. Evaluate the effect of different management systems on the labile and stable organic matter pools.

2.3 Methods

2.3.1 Site description

The study region is based within the Manu Biosphere Reserve in the south-eastern Peruvian Andes. Different land uses were chosen from three distinctively different ecosystems along an elevation transect through the Koñsnipata Valley; ranging from high altitude montane grassland (3200 m a.s.l, colloquially referred to as 'Puna'), the upper montane forest (2200 - 3200 m a.s.l), down to premontane tropical forest (500 - 1200 m a.s.l). Twenty three sites were sampled in total, which comprised different land uses along the altitudinal gradient. A summary of site history and location for the all sites can be found in Table 2.1 and Figures 2.1 and 2.2.

The undulating terrain in the montane grassland is commonly used by the local communities for extensive cattle grazing and although the study area is in the National Park, burning and grazing still occasionally takes place. In order to investigate the effects of burning and grazing on soil C stocks, we took advantage of an ongoing burning/grazing study that was established in July-August 2010 (Oliveras et al., 2014). This included two sites that were identified as being burnt in 2003 (Wayqecha) and 2005 (Acjanaco) (Table 2.1). The earlier history of burning was unknown for Wayqecha but for Acjanaco, prior to the burn in 2005, this area had not been exposed to burning since the 1970s. The site at Wayqecha was located at approximately 3085 m a.s.l. in Wayqecha Biological Station (13°18´S, 71°58´W), where the mean annual precipitation is 1560 mm and mean annual air temperature is 11.8 °C (Girardin et al., 2013). The site at Acjanaco (13°17'S, 71°63´W), was located on the Manu national park boarder at 3400 m a.s.l and had a mean annual precipitation of 760 mm and mean annual air temperature 6.8 °C. The wet season ran from October to March and there were more noticeable variations in diurnal temperatures than seasonal differences (Zimmermann et al., 2009b). Grass species composition was similar on both sites (*Calamagrostis longearistata, Scirpus rigidus and Festuca dolichophylla) (Oliveras et al., 2014)* and the soils were typically only 30 cm deep with an acidic organic rich A layer and stony B/C horizons (Zimmermann et al., 2009b; Gibbon et al., 2010).

In the tropical montane cloud forest, sites were chosen near the boundary between the cloud forest treeline and the puna, where the presence of burning was likely to be the result of montane grassland fires

spreading into the cloud forest. Three sites, with different burning years, were chosen: Wayqecha in 2003 (3025 m a.s.l, 13°11´S, 71°35´W), Acjanaco in 2005 (3400 m a.s.l, 13°10'S, 71°38'W) and Sunchubamba in 2010 (3200 m a.s.l, 13°12'S, 71°35'W) (Table 2.1). The mean annual temperature at this elevation was 12.5 °C with 1710 mm mean annual precipitation (Girardin et al., 2010). The sites were characteristically very steep with soils being acidic Palaeozoic shales-slates with an Oh horizon of approximately 20-30 cm, consisting of dense fine root mesh and partly decomposed plant material (Zimmermann et al., 2009a; Robertson et al., 2010).

The study area in the premontane rainforest was located at Villa Carmen Biological Reserve, which is a 3070 ha abandoned farm, recently purchased by La Asociación para la Conservación de la Cuenca Amazónica (ACCA), situated at the confluence of the Rio Pini Pini and Rio Tono rivers. The terrain on which the sites were chosen was relatively flat and the mean annual temperature at this elevation was 22 °C with 4500 mm mean annual precipitation. Nine land uses were chosen at this elevation: mature forest (V - F); selectively logged forest (V - SL); secondary forest (V - SF); abandoned banana (V - AB); cultivated banana (V - B); pineapple (V-PA); low intensity grazed pasture (V - P); high intensity grazed pasture (V-P1); abandoned pasture (V-P2) (Table 2.1).

The secondary forest site was cleared and transformed into a rice plantation more than twenty five years ago (method of clearing unknown), and was abandoned fifteen years ago. The secondary forest is now dominated by bamboo with a very dense understory. The selectively logged forest never ceased to be a forest but has a more open canopy and commercially valuable trees missing, such as: *Iriartea deltoid*, which is extensively used in construction and *Euterpe precatoria*, which is used for extraction of palm (*personal communication with the manager of Villa Carmen; Dr Adrian Tejedor*). The banana sites were cleared using the slash and mulch method with regular clearing of understory regrowth and no history of fertilizer use (*Dr Adrian Tejedor*). The abandoned banana site was abandoned in 2003 and now has the appearance of a forest with a few banana trees still present and little undergrowth but the original drainage channels are still noticeable. The currently cultivated banana site has been active for the last five years and is still being cleared every year for regrowth. The pineapple plantation has not been used for cultivation in the last five years but is still dominated by pineapple plants with trees interspersed. The

method and time of clearing are unknown. All the pasture sites were cleared more than ten years ago but the exact timing and method of clearing are unknown. The low intensity grazed pasture site has been used intermittently for periods of cattle grazing (3 months at a time); the high intensity grazed pasture was constantly exposed to cattle and horse grazing throughout the year; grazing stopped on the abandoned pasture at least five years ago and there are now trees present.

Table 2.1 Site and soil description for all twenty three sites in the montane grassland, tropical montane cloud forest and premontane rainforest

Ecosystem	Site code	Site name	Dominant vegetation	Site history	Elevation (m a.s.l)	Annual precip. (mm)	Mean Temp. (° C)
Montane grassland	WP - BG	Wayqecha puna grazed-burnt	*Calamagrostis longearistata; Scirpus rigidus; Festuca dolichophylla*	Burnt in 2005	3121	1560	11.8
	W P- GNB	Wayqecha puna grazed- non burnt		No burning			
	WP - NGB	Wayqecha puna non grazed-burnt		Burnt in 2005			
	WP - NBNG	Wayqecha puna non grazed- non burnt		No burning			
	AP - BG	Acjanaco puna grazed-burnt		Burnt in 2003	3400	760	6.8
	AP - GNB	Acjanaco puna grazed- non burnt		No burning			
	AP - NGB	Acjanaco puna non grazed-burnt		Burnt in 2003			
	AP - NBNG	Acjanaco puna non grazed- non burnt		No burning			
Montane cloud forest	W - B	Wayqecha - burnt	*Weinmannia crassifolia; Clusia flaviflora; Clusia alata*	Burnt in 2003	3025	1710	12.5
	W - NB	Wayqecha - non burnt		No burning			
	A - B	Acjanaco - burnt		Burnt in 2005	3400		
	A - NB	Acjanaco - non burnt		No burning			
	S - B	Sunchubamba - burnt		Burnt in 2010	3200		
	S - NB	Sunchubamba - non burnt		No burning			
Premontane rainforest	V - F	Mature forest	*Precatoria; Guaduinae*	No signs of disturbance.	580	4500	22
	V - SL	Selectively logged forest	*Guadu;Iriartea deltoid; Socratea exorrhiza*	Never ceased to be a forest.	541		
	V - SF	Secondary forest		Abandoned rice plantation 25 years ago.	565		
	V - B	Banana cultivation	Musa paradisiaca	Slash and mulch - no burning or fertilizer.	527		
	V - AB	Abandoned banana		Cultivation stopped 8 years ago - no burning or fertilizer history.	521		
	V - PA	Pineapple	Ananas comosus	Pineapple and trees present			
	V - P	Pasture - low intense	*Poaceae*	Low intense cattle grazing	508		
	V - P1	Pasture - intense	*Brachiaria*	Intense cattle grazing			
	V - P2	Pasture - abandoned		No grazing and trees present			

Dominant vegetation for the puna and upper montane cloud forest were taken from (Oliveras et al., 2014) and for premontane land uses the vegetation was recorded by Adrian Tejedor (a full list species can be found in Appendix 1.1, Table 1.1)

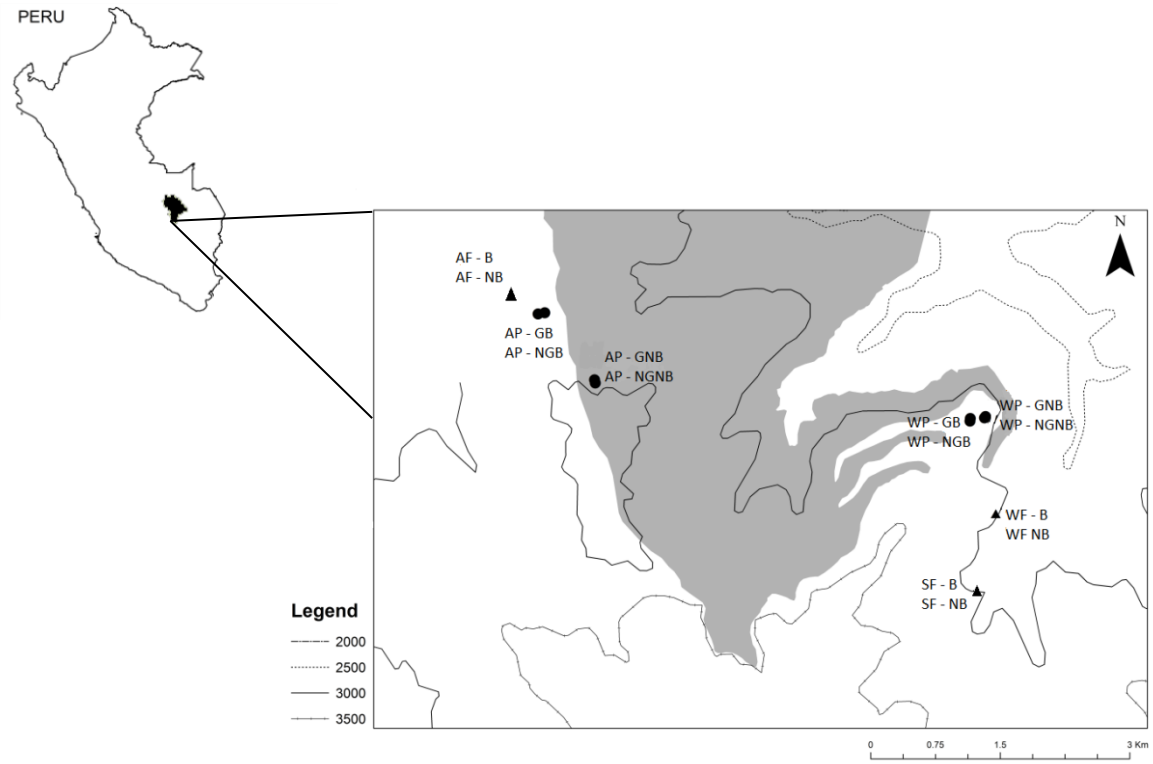


Table 2.1 Map of the sites in the upper montane cloud forest (triangles) and high elevation montane grassland (circles) (adapted from (Oliveras et al., 2014). Grey area represents the Manu National Park.

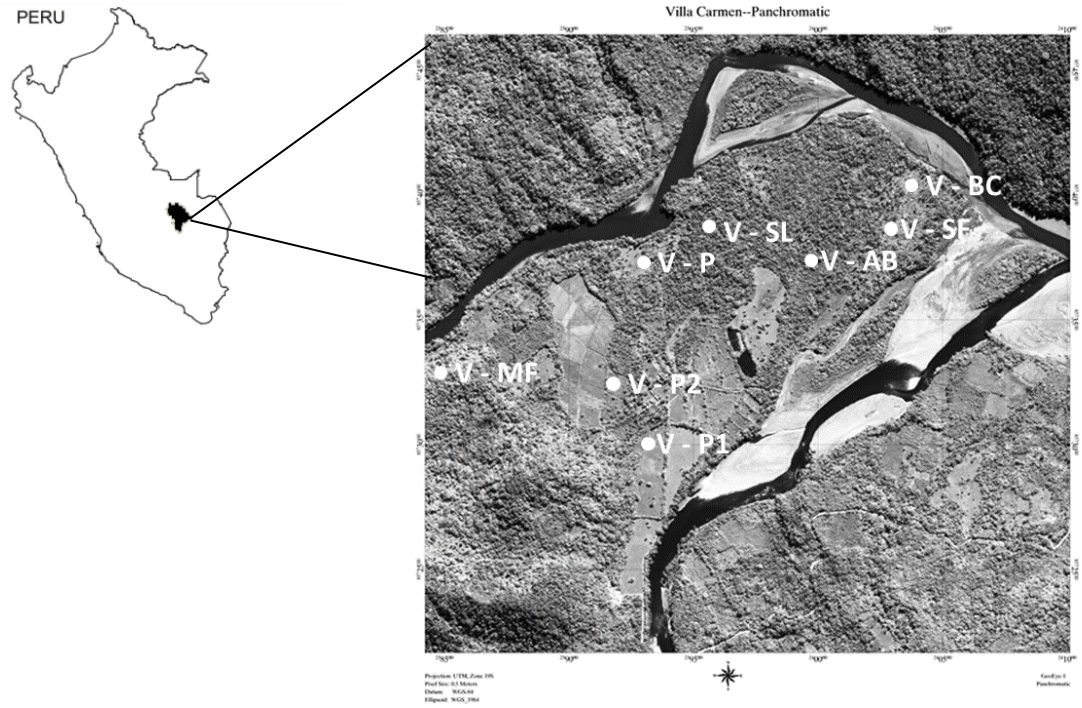


Table 2.2 Map of the sites in the premontane forests at Villa Carmen (collected by the (GeoEye-1-satellite, 1984).

2.3.2 Sample design

Different sampling designs were applied to the montane grassland, montane cloud forest and premontane rainforest and for the purpose of statistical analysis the elevation bands are reported separately. The sites in the montane grassland were set up in a factorial design, with burnt and adjacent non burnt plots (no more than 300 metres), which were then split into two subplots; one with fencing constructed to stop cattle grazing and one left unfenced. Each site therefore had a plot that was: burnt - non grazed; burnt - grazed; non burnt - grazed and non burnt - non grazed. In the montane cloud forest, each burnt plot had a paired non burnt plot for comparison (no more than 30 metres away), in the premontane forest, the different land uses were compared to each other and to the mature forest control plot. The sites were within 8 km of each other, apart from the mature forest which was approximately 16 km away from the agricultural plots.

2.3.3 Soil sampling and analysis

Soil sampling: soil samples were taken during the dry season in July 2012 with six replicates at 0-5, 5-10, 10-20 and 20-30 cm depths on each site. Sampling was achieved by digging six soil pits randomly located within each site and taking approximately 50 g of soil from each depth. Soil samples were air-dried and sieved with a 2 mm mesh sieve before being shipped to the University of St Andrews for all further analysis (Hairiah et al., 1995; Brown, 1982). In the premontane sites, further sampling down to 1 metre was carried out but this included only one replicate and was not included in statistical analysis.

Bulk density: soil bulk density was determined by the soil core method (Black and Hartge, 1986). Undisturbed soil cores (30 cm^3) were taken from three of the soil pits at 0-10, 10-20 and 20-30 cm. The samples were dried at 105 °C for 48 hours and bulk density was estimated as the mass of oven-dry soil divided by the core volume. Bulk density for the upper montane cloud forest and puna soils were taken from (Oliveras et al., 2014; Zimmermann et al., 2009c) (puna 0-10 cm = 0.40 g cm^{-3}, puna 10-20 cm = 0.54 g cm^{-3} and cloud forest 0-10 cm = 0.03 g cm^{-3}, 10-20 cm = 0.41 g cm^{-3}).

Soil fractionation: a method developed by (Mueller and Koegel-Knabner, 2008) and (Marìn-Spiotta et al., 2008) for soil fractionation was used, which combined a density and particle-size fractionation. This method is useful for separating SOM based on the location within the soil matrix and the degree of association with minerals. Prior to the experiment a sub sample of soil was taken for moisture correction. The air dried soil material (15 g < 2 mm) was saturated with 60 mL sodium polytungstate solution (NaPT, Na6 [$H_2W_{12}O_{40}$], Sometu-Germany) at a density of 1.85g/mL and centrifuged for 45 minutes at 3600 rpm and allowed to settle overnight. The floating free light fraction (free LF) was aspirated via a pump and rinsed with 500 mL of deionised water through a 0.4 µm polycarbonate filter (Whatman Nuclepore Track Etch Membrane) to remove residual NaPT. The remaining slurry was further saturated with 60 mL sodium polytungstate solution (1.4 g cm^{-3}), mixed using a benchtop mixer (Mixer/Vortexer - BM1000) for 1 minute at 3200 rpm and dispersed ultrasonically (N10318 Sonix VCX500 sonicator Vibra-cell ultrasonic processor) for 3 min at 70 % pulse for a total input of 200 J/mL. Centrifugation (45 minutes at 3600 rpm) was used to separate the occluded light fraction (occluded LF) from the mineral residue and allowed to sit overnight to achieve further separation by flotation of organic debris and settling of clay particles in solution. The occluded LF was then aspirated via a pump and rinsed. In order to remove the NaPT from the heavy fraction (heavy F), deionised water was mixed with the material and centrifuged for 15 minutes at 4000 rpm 5 times. All fractions were oven dried at 100 °C overnight, weighed and physically ground to a fine powder before C analysis and isotope analysis.

Carbon and isotope analysis: bulk soils were ground and homogenised using a grinding mill (Planetary Mono Mill PULVERISETTE) in preparation for C and isotope analysis at the University of St Andrews laboratories using a Finnegan Delta plus XP gas source mass spectrometer coupled to an elemental analyser (EA-IRMS). Every ten samples, a duplicate sample was run with a duplicate error < 5% to test for instrumental precision. Classified standards were used (B2176, B2151, B2153 and sucrose) and all isotopes were expressed as $\delta^{13}C_{V\text{-}PDB}$; the isotopic composition of the reference gas used is -32.79 ‰ $\delta^{13}C_{V\text{-}PDB}$. Total soil C was calculated as follows:

SOC = BD x C content x D [Eq. 1]

Where SOC is the soil organic carbon content (g C m^{-2}), BD is soil bulk density (kg m^{-3}), C is the soil carbon content (g C kg^{-1}) and D is the soil sampling depth (m).

Calculations for the fraction of soil C originating from pasture grasses were based on a two-component mixing model (Balesdent et al., 1988):

$$FC_B = (\delta_X - \delta_A) / \delta_{vegB} - \delta_A), \quad \text{[Eq. 2]}$$

Where FC_B is the fraction of new soil C, δ_X is the $\delta^{13}C$ of the bulk soil, δ_A is the $\delta^{13}C$ of the original vegetation and δ_{vegB} is the $\delta^{13}C$ value of the new plant inputs to the soil. The $\delta^{13}C$ of plant material was taken was from (Marin-Spiotta et al., 2009) (pasture grass = -16 ± 1.1 ‰ and primary forest litter (-29.5 ± 0.7 ‰).

2.3.4 Statistical analysis

The three regions were analysed separately due to the confounding statistical effects that might occur due to the differing climates, soils and vegetation variation along the elevation gradient. Statistical analyses were performed using the R 3.0.2 (R Core Team, 2012) and significance reported at $p < 0.05$. The data were normally distributed when checked using the Shapiro-Wilk test. Analysis of variance (ANOVA) with Tukey's Honest Significant Difference (HSD) post hoc test were used to examine statistically significant differences between means of $\delta^{13}C$ values and C concentrations of bulk and soil fractions among the different land uses within the three different elevations.

2.4 Results

2.4.1 Belowground C stocks

Grazing and burning in high elevation montane grasslands

Grazing, burning and the combination of burning and grazing did not significantly alter total soil C at any depth down to 30 cm (Table 2.2). The overall sum of all the measured depths showed signs of a decrease in C stocks on the grazed soils, although this was not significant. Soil C concentrations were highest in the top 5 cm and decreased with depth on all land uses. On average, Acjanaco (2003) had significantly higher C stocks (48.8 ± 17.1 Mg C ha^{-1}) compared to Wayqecha (2005) (34.8 ± 19.1 Mg C ha^{-1}) but neither site had any significant differences among the land uses so the data were pooled.

Table 2.2 Bulk soil mean C concentrations (%), C content (Mg C ha^{-1}) for each depth and total C stocks (0-30 cm) in the upper montane grasslands

Land use	Depth (cm)	Bulk C concentration (%)	Bulk C (Mg C ha^{-1})
G - B (Grazed – burnt)	0-5	20.2 ± 1.5[a]	40.5 ± 3.0[a]
G - NB (Grazed - non burnt)		20.8 ± 2.7[a]	41.3 ± 5.3[a]
NG - B (Non grazed - burnt)		23.5 ± 1.9[a]	46.9 ± 3.9[a]
NG - NB (Non grazed - non burnt)		19.8 ± 2.2[a]	43.4 ± 3.2[a]
G - B	5-10	14.9 ± 1.2[a]	29.7 ± 2.5[a]
G - NB		17.9 ± 2.6[a]	35.9 ± 5.1[a]
NG - B		16.4 ± 2.2[a]	34.0 ± 4.5[a]
NG - NB		18.9 ± 2.1[a]	37.7 ± 4.3[a]
G - B	10-20	7.7 ± 1.1[a]	41.6 ± 6.1[a]
G - NB		8.9 ± 1.5[a]	47.9 ± 7.9[a]
NG - B		13.6 ± 2.2[a]	69.7 ± 10.0[a]
NG - NB		12.7 ± 2.7[a]	59.0 ± 8.4[a]
G - B	20-30	4.1 ± 1.6[a]	26.4 ± 8.7[a]
G - NB		4.4 ± 2.2[a]	23.6 ± 10.6[a]
NG - B		7.8 ± 3.2[a]	19.0 ± 4.6[a]
NG - NB		8.0 ± 2.7[a]	43.2 ± 14.2[a]
G - B	0-30	12.6 ± 6.8[a]	149 ± 35[a]
G - NB		14.7 ± 7.9[a]	149 ± 38[a]
NG - B		15.2 ± 8.1[a]	175 ± 41[a]
NG - NB		14.9 ± 7.3[a]	183 ± 62[a]

Different letters down the columns within each depth represent significant differences among sites. All values are given with 1 standard error of the mean (n = 3).

When averaging the four depths, burning and grazing had a significant negative effect on the proportion of C in the free LF (Table 2.3). However, when analysing the depths individually, there was only a significant loss of C in the free LF at 10-20 and 20-30 cm depth, with a reduction of ~ 16 % (Figure 2.3 and Appendix 1.1, Table 1.2). When analysing the two sites separately, the grazed-burnt soils at Wayqecha had a significantly smaller proportion of C in the free LF at 0-5 cm (p-value = 0.002), whereas

at Acjanaco there were no significant differences among the land uses (refer to Appendix 1.1, Table 1.3). The mass of soil recovered in the free LF was significantly lower in the grazed-burnt soils at 0-5 cm (p-value = 0.002).

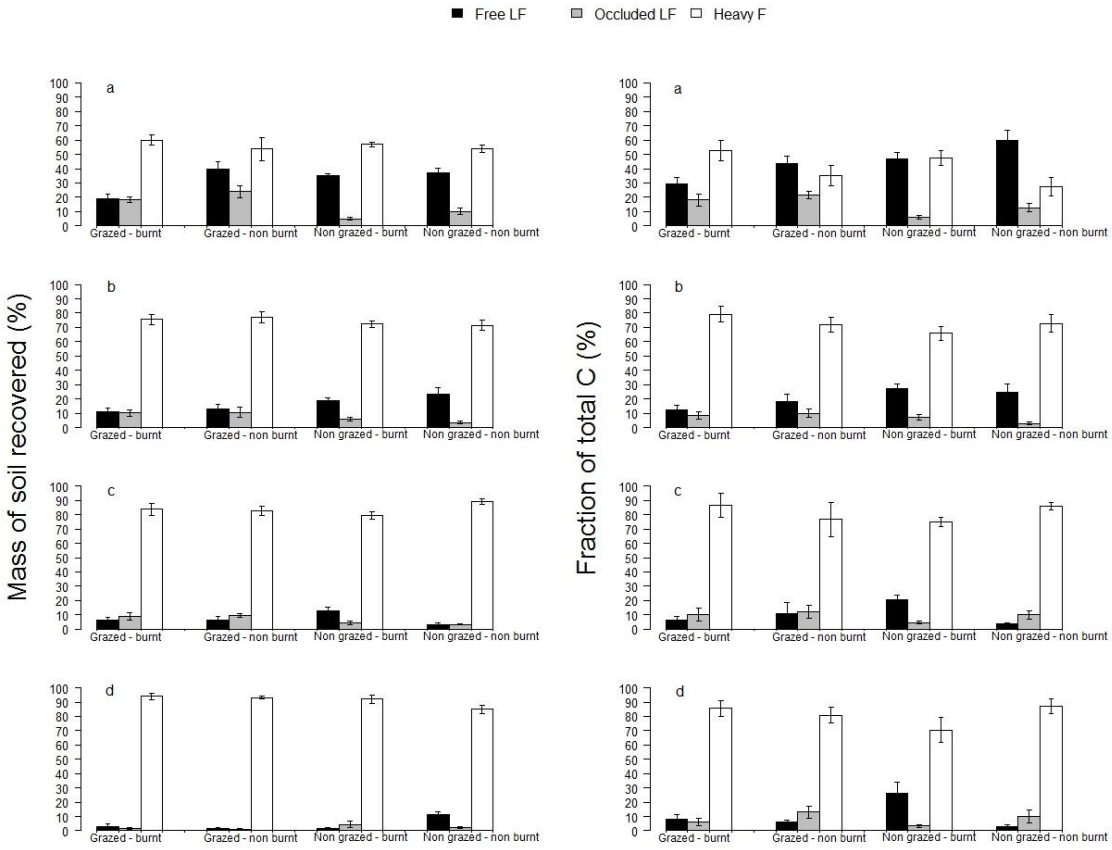


Figure 2.3 Mass of soil recovered in the three density fractions (%) on the four left bar plots and the proportion of total C residing in the three density fractions (%) on the four right bar plots for the different land uses in the montane grasslands (a = 0-5 cm, b = 5-10 cm, c = 10-20 cm, d = 20-30 cm). Error bars indicate 1 standard error of the mean (n = 6).

When combining the soil profile (0-30 cm), the free LF in the control soils made 20 % of the bulk soil mass and 30 % of the soil C content compared the burnt-grazed soils, which had the smallest recovery of free LF (10 %) and had significantly lower C content (14 %) (Table 2.3).

Table 2.3 Mean mass recovery of density fractions and proportion of total C residing in the three density fractions (%) from the total soil profile (0-30 cm) for upper montane grasslands. Different letters down the columns represent significant differences.

	Free LF		Occluded LF		Heavy F	
	Fraction of total C (%)	**Mass of soil recovered (%)**	**Fraction of total C (%)**	**Mass of soil recovered (%)**	**Fraction of total C (%)**	**Mass of soil recovered (%)**
GB	14.0 ± 5.3^{b}	9.9 ± 3.6^{a}	10.8 ± 2.6^{ab}	9.8 ± 3.4^{ab}	76.0 ± 8.0^{a}	78.4 ± 7.2^{a}
GNB	22.7 ± 13.3^{ab}	16.2 ± 8.5^{a}	8.9 ± 2.1^{bc}	5.3 ± 1.6^{bc}	68.3 ± 14.0^{a}	76.7 ± 8.1^{a}
NGB	19.7 ± 8.3^{ab}	15.1 ± 8.5^{a}	14.2 ± 2.5^{a}	11.3 ± 4.7^{a}	66.1 ± 10.5^{a}	76.6 ± 8.3^{a}
NGNB	30.0 ± 5.7^{a}	19.5 ± 5.5^{a}	5.2 ± 0.8^{c}	4.3 ± 0.7^{c}	64.7 ± 6.1^{a}	69.7 ± 5.8^{a}

Upper montane forest

Burning did not significantly alter total soil C at any depth down to 30 cm when combing the three sites (Table 2.4). The burnt plot at Wayqecha was the only site to have a significant loss of soil C at 0-5 and 10-20 cm. Soil C concentrations were significantly lower in the top 10 cm and increased with depth as the bulk density increased on all the sites. The density fractionation technique used in this study was not appropriate for the high organic matter content of the surface O horizon and so was not applied to the upper montane forest soils.

Table 2.4 Total soil mean C concentrations (Mg C ha^{-1}) for upper montane cloud forest. Different letters down the columns within each depth represent significant differences among sites. All values are given with 1 standard error of the mean (n = 3).

Site	**Land use**	**0-5 cm**	**5-10 cm**	**10-20 cm**	**20-30 cm**	**0-30 cm**
Wayqecha (2003)	Burnt	3.0 ± 0.8^{a}	3.7 ± 0.2^{a}	39.7 ± 11.4^{a}	39.5 ± 14.4^{a}	120 ± 12
	Non-burnt	6.0 ± 0.2^{b}	5.2 ± 1.1^{a}	130.6 ± 25.5^{b}	82.2 ± 12.9^{a}	168 ± 20
Acjanaco (2005)	Burnt	5.5 ± 0.3^{a}	2.8 ± 0.7^{a}	46.2 ± 10.5^{a}	40.3 ± 6.4^{a}	95 ± 13
	Non burnt	6.5 ± 0.7^{a}	4.0 ± 0.6^{a}	61.6 ± 6.9^{a}	45.0 ± 6.4^{a}	150 ± 19
Sunchubamba (2010)	Burnt	7.4 ± 0.2^{a}	5.7 ± 0.5^{a}	95.2 ± 21.5^{a}	37.9 ± 15.7^{a}	163 ± 16
	Non burnt	7.6 ± 0.2^{a}	7.3 ± 0.5^{a}	86.8 ± 13.5^{a}	64.6 ± 10.2^{a}	167 ± 29
COMBINED SITES	BURNT	5.3 ± 0.7^{a}	4.1 ± 0.5^{a}	60.4 ± 11.6^{a}	39.2 ± 5.6^{a}	114 ± 45
	NON BURNT	6.7 ± 0.3^{a}	5.5 ± 0.6^{a}	93.8 ± 13.8^{a}	64.0 ± 7.2^{a}	169 ± 64

Premontane forest

Land-use did not significantly alter soil C concentrations in the very surface soil (0-5 and 5-10 cm) but total C stocks of the summed depth down to 30 cm resulted in significantly lower C stocks in the cultivated banana soils and low intensity grazed soils (Table 2.5). Although not significant, the highest SOC values were measured on the abandoned pasture, high intensity grazed pasture and pineapple soils. Average soil bulk density did not differ significantly among the land uses. Soil particle size distribution determined that the mature forest, pasture, and selectively logged forest were sandy loams and the secondary forest, abandoned banana and cultivated banana were silty loams (Appendix 1.1, Table 1.4).

Table 2.5 Bulk soil mean C concentrations (Mg C ha^{-1}) from 0-5 cm and total C stock (0-100 cm) across all land use sites in the premontane elevation.

Land use	Bulk C stock 0-5 cm (Mg C ha^{-1})	C stock 0-30 cm (Mg C ha^{-1})	C stock 0-100 cm (Mg C ha^{-1})	% C in top 10 cm	Bulk density (g cm^{-3})
VC - F (mature forest)	7.4 ± 1.2^{a}	28.4 ± 2.4^{ab}	61.8 ± 2.5^{a}	21 %	0.99 ± 0.01^{a}
VC - SL (logged)	6.6 ± 1.3^{a}	23.3 ± 1.3^{bcd}	29.5 ± 1.1^{bc}	38 %	1.06 ± 0.02^{a}
VC - SF (secondary)	6.7 ± 0.6^{a}	22.6 ± 1.9^{bcd}	37.2 ± 2.0^{b}	25 %	0.92 ± 0.02^{a}
VC - AB (abandoned banana)	6.4 ± 1.3^{a}	20.4 ± 1.9^{bcd}	28.8 ± 1.7^{c}	35 %	1.05 ± 0.02^{a}
VC - B (banana)	4.6 ± 0.6^{a}	16.3 ± 0.5^{d}	27.0 ± 0.6^{bc}	35 %	NA
VC - PA (pineapple)	9.7 ± 1.5^{a}	29.1 ± 1.6^{ab}	61.9 ± 1.6^{a}	26 %	0.92 ± 0.04^{a}
VC - P (low intensity)	4.8 ± 0.8^{a}	19.1 ± 1.7^{cd}	28.6 ± 1.7^{bc}	24 %	1.01 ± 0.01^{a}
VC - P1 (high intensity)	9.1 ± 0.9^{a}	28.4 ± 0.2^{abc}	NA	NA	NA
VC - P2 (abandoned)	10.7 ± 2.1^{a}	36.1 ± 1.4^{a}	67.8 ± 1.9^{a}	NA	NA

Different letters down the columns within each depth represent significant differences among sites. All values are given with 1 standard error of the mean (n = 6). Bulk C stock down to 100 cm in VC - P1 (low intensity grazing) could not be calculated due to soil sampling limitations. Bulk densities are given with 1 standard error of the mean (n = 3).

The proportion of C in the three density fractions did not differ to the mature forest among the land uses, with the exception that the pineapple soils had significantly lower free LF in the very surface soils (0-5 and 5-10 cm) and the cultivated banana soils had a significantly higher proportion of occluded LF at 5-10, 10-20 and 20-30 cm depths and significantly lower heavy F at 20-30 cm (Appendix 1.1, Table 1.5). Further down the soil profile, the general trend for most of the sites was a decrease in the proportion of C in the free LF and occluded LF (Figure 2.4). When analysing the full soil (0-30 cm), the pineapple soils had significantly smaller proportions of free and occluded LFs, whereas the cultivated banana soils had significantly higher proportions of occluded F compared to the mature forest. The lowest proportion of heavy F was measured on both banana soils with ~ 16 % less heavy F than the mature forest, although this was not significant (Table 2.6).

Table 2.6 Mean mass recovery of density fractions and proportion of total C residing in the three density fractions (%) from the total soil profile (0-30 cm). Different letters down the columns represent significant differences among the premontane sites.

	Free LF		Occluded LF		Heavy F	
	Fraction of total C (%)	Mass of soil recovered (%)	Fraction of total C (%)	Mass of soil recovered (%)	Fraction of total C (%)	Mass of soil recovered (%)
VC - F	12.1 ± 2.6^{ab}	1.6 ± 0.5^{a}	12.4 ± 3.0^{bc}	2.7 ± 0.8^{a}	75.5 ± 5.3^{ab}	99.2 ± 0.5^{ab}
VC - SL	10.8 ± 6.0^{abc}	1.2 ± 0.8^{a}	13.1 ± 4.6^{bc}	1.5 ± 0.6^{ab}	76.1 ± 10.0^{ab}	100.8 ± 1.6^{a}
VC - SF	10.2 ± 2.4^{abc}	0.9 ± 0.4^{a}	13.5 ± 2.1^{bc}	1.0 ± 0.4^{b}	76.9 ± 4.0^{ab}	98.2 ± 0.5^{b}
VC - AB	15.7 ± 2.4^{a}	1.5 ± 0.6^{a}	19.1 ± 2.3^{ab}	2.1 ± 0.7^{ab}	65.2 ± 4.3^{b}	97.5 ± 0.1^{b}
VC - B	11.0 ± 2.4^{ab}	1.2 ± 0.5^{a}	24.6 ± 3.1^{a}	2.2 ± 0.6^{ab}	64.3 ± 1.8^{b}	97.6 ± 0.8^{b}
VC - PA	2.8 ± 0.1^{c}	0.7 ± 0.2^{a}	8.7 ± 1.2^{c}	1.9 ± 0.3^{ab}	88.5 ± 1.1^{a}	97.4 ± 0.7^{b}
VC - P	6.8 ± 0.7^{bc}	0.9 ± 0.3^{a}	11.8 ± 0.8^{bc}	1.1 ± 0.3^{b}	79.8 ± 1.5^{a}	96.1 ± 0.2^{b}
VC - P1	9.8 ± 3.7^{abc}	1.5 ± 0.3^{a}	11.7 ± 3.6^{bc}	2.7 ± 0.3^{ab}	79.4 ± 3.5^{ab}	94.7 ± 1.8^{b}
VC - P2	6.1 ± 1.7^{bc}	0.8 ± 0.3^{a}	10.0 ± 2.3^{bc}	1.9 ± 0.3^{ab}	82.2 ± 4.2^{a}	98.8 ± 1.4^{ab}

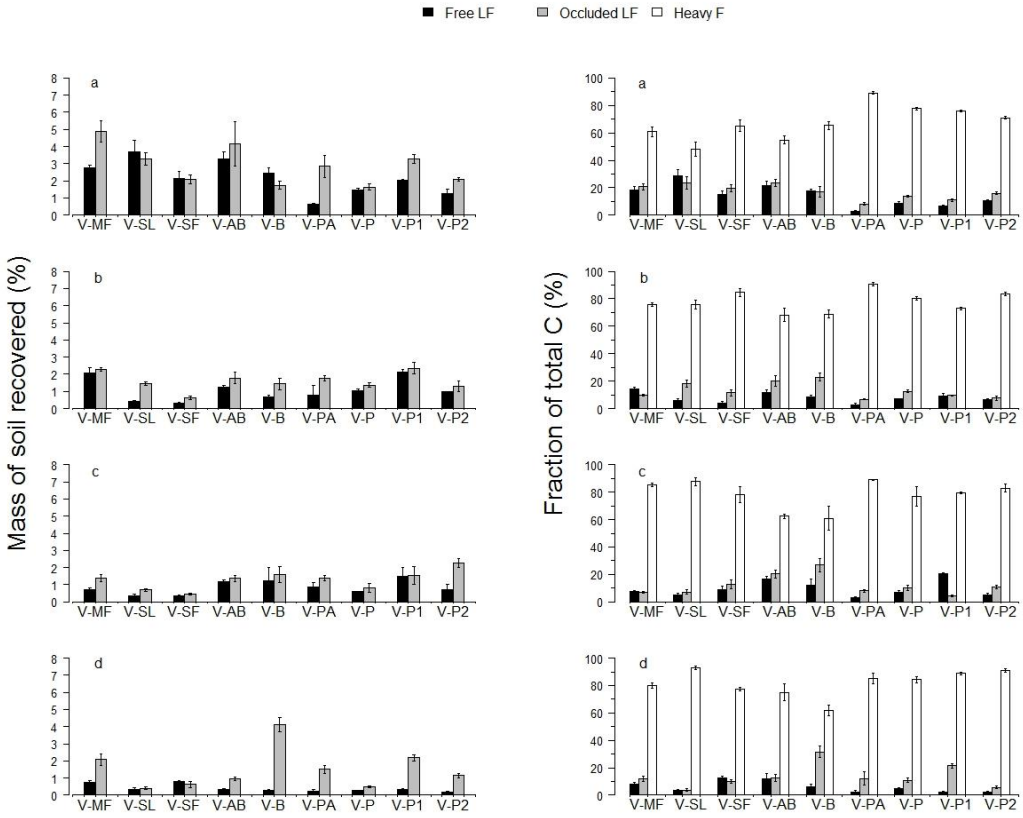


Figure 2.4 Mass of soil recovered in the three density fractions (%) on the four left bar plots and the proportion of total C residing in the three density fractions (%) on the four right bar plots for the different land uses in the premontane elevations (a = 0-5 cm, b = 5-10 cm, c = 10-20 cm, d = 20-30 cm). Error bars indicate standard 1 error of the mean (n = 6).

2.4.2 Natural abundance stable isotope measurements in premontane pasture soils

Bulk soil $\delta^{13}C$ concentrations differed significantly between the low intensity grazed pasture and mature forest at all depths. The high intensity grazed pasture had similar bulk soil $\delta^{13}C$ concentrations to the mature forest at all depths, whereas the abandoned pasture was more enriched in the surface soil layers (Table 2.7). The low intensity grazed pasture became progressively more depleted in $\delta^{13}C$ with depth, ranging from -18.9 ± 0.5 at 0-5 cm to -22.7 ± 1.1 (‰) at 0-30 cm. The high intensity grazed pasture and abandoned pasture had a smaller range of -24.9 ± 0.2 to -23.1± 5.2 and -26.6 ± 0.4 to -26.4 ± 0.2 (‰), respectively.

The three density fractions in the low intensity grazed soils were significantly enriched in $\delta^{13}C$, which gradually depleted with depth and to a point where the heavy F was not significantly different to the

mature forest. The high intensity grazed and abandoned pastures were significantly enriched in $\delta^{13}C$ in the free LF at all depths and also in the occluded LF at 0-10 cm in high intensity grazed soils. There were no significant differences in the heavy F between the mature forest and high intensity grazed and abandoned pasture soils.

Table 2.7 Mean stable isotopes in bulk and density soil fractions from 0-30 cm depth on three pastures and mature forest.

Land use	Depth (cm)	Bulk $\delta^{13}C$ (‰)	Free LF $\delta^{13}C$ (‰)	Occluded LF $\delta^{13}C$ (‰)	Heavy F $\delta^{13}C$ (‰)
VC - F (mature forest)	0-5	-28.9 ± 0.1^{c}	-29.4 ± 0.0^{d}	-28.5 ± 0.6^{c}	-25.6 ± 1.1^{b}
VC – P (low intensity)		-18.9 ± 0.5^{a}	-15.9 ± 0.2^{a}	-17.8 ± 0.2^{a}	-17.9 ± 0.2^{a}
VC - P1 (high intensity)		-26.6 ± 0.4^{bc}	-19.3 ± 1.4^{b}	-22.9 ± 1.1^{b}	-24.9 ± 2.1^{b}
VC - P2 (abandoned)		-24.9 ± 0.2^{b}	-26.1 ± 0.2^{c}	-27.2 ± 0.1^{c}	-26.8 ± 0.5^{b}
VC - F	5-10	-28.3 ± 0.1^{c}	-29.3 ± 0.2^{d}	-28.2 ± 0.6^{c}	-27.0 ± 0.9^{b}
VC - P		-19.6 ± 0.5^{a}	-16.1 ± 0.5^{a}	-18.6 ± 0.5^{a}	-18.7 ± 0.2^{a}
VC - P1		-26.4 ± 0.2^{bc}	-20.6 ± 0.2^{b}	-24.9 ± 0.8^{b}	-25.4 ± 1.3^{b}
VC - P2		-26.1 ± 0.8^{b}	-26.0 ± 0.3^{c}	-26.3 ± 0.5^{bc}	-26.6 ± 0.1^{b}
VC - F	10-20	-27.8 ± 0.5^{b}	-28.9 ± 0.5^{d}	-28.2 ± 1.5^{b}	-26.8 ± 0.4^{b}
VC - P		-21.2 ± 1.4^{a}	-18.1 ± 0.7^{a}	-20.7 ± 0.9^{a}	-20.8 ± 1.3^{a}
VC - P1		-26.2 ± 0.4^{b}	-21.6 ± 0.4^{b}	-24.9 ± 1.4^{b}	-26.3 ± 0.4^{b}
VC - P2		-26.2 ± 1.3^{b}	-26.2 ± 0.3^{c}	-26.3 ± 1.0^{b}	-25.8 ± 1.1^{b}
VC - F	20-30	-27.4 ± 0.4^{b}	-28.7 ± 0.4^{c}	-27.6 ± 1.5^{b}	-25.3 ± 2.1^{a}
VC - P		-22.7 ± 1.1^{a}	-18.3 ± 2.6^{a}	-21.8 ± 0.7^{a}	-23.9 ± 2.0^{a}
VC - P1		-26.4 ± 0.2^{ab}	-20.7 ± 0.1^{ab}	-25.4 ± 0.5^{b}	-26.4 ± 0.2^{a}
VC - P2		-23.1± 5.2^{ab}	-26.2 ± 0.2^{bc}	-27.9 ± 0.5^{b}	-26.8 ± 0.1^{a}

Different letters down the columns within density fraction type and depth represent significant differences between sites. Values are given with 1 standard deviation of the mean. Mature forest (n = 6) and pasture soils (n = 3).

When estimating the contribution of pasture-derived C to bulk soil, the low intensity grazed pasture had the most grass-derived C, especially in the surface layers. The high intensity grazed and abandoned pasture had the least grass-derived C, which continued to decrease with depth until almost all the soil C was C3 forest vegetation (Figure 2.5).

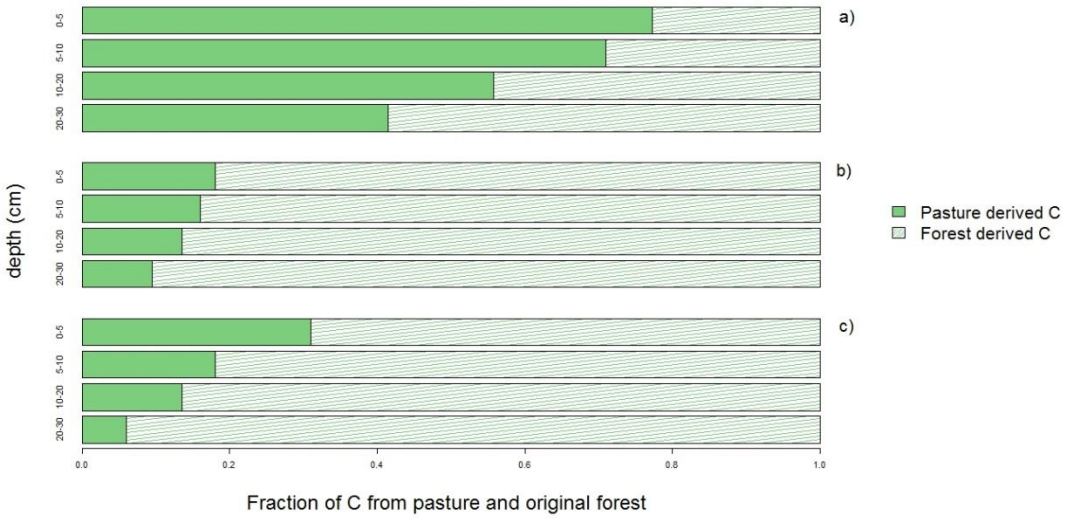


Figure 2.5 Contribution of pasture-derived C to bulk soil with depth from three pasture soils: a) low intensity grazing (VC - P); b) high intensity grazing (VC - P1); c) abandoned pasture (VC - P2).

2.5 Discussion

2.5.1 Soil C stocks

No difference in soil C stocks with burning and grazing in montane grasslands

The effect of burning and grazing did not significantly alter total soil C content, although the proportion of C in the free LF was significantly reduced with the combination of burning and grazing when averaging the four depths because of a significant loss of C at 10-30 cm. As the free LF accounts for only a small proportion of the total C content (14 - 30 %), the discernible loss of C in the free LF can be undetected in the total C content. In this study, the loss of C from grazing and burning only accounted for ~ 5 % of the total C, which is within the error of our measurements. Changes to this highly dynamic free LF have been highlighted in other land management studies and are an early indication of changes in SOC quantity and quality (Six et al., 2002b; Wang and Fang, 2009), as it can sometimes takes many years before significant changes are detected in the total SOC (Hassink et al., 1997; Soon et al., 2007; Gong et al., 2009). Overall, large total SOC stocks were measured in these montane grasslands, which is in keeping with Páramo and other high elevation grassland studies (Hofstede, 1995; Zimmermann et al., 2009c; Li et al., 2013; Muñoz et al., 2013) and are probably attributable to low temperatures and wet conditions causing slow mineralisation of SOM and turnover rates.

The negligible effect of burning on total soil C may be a consequence of low intensity fires, fire-resilient grasses, and potentially low fuel loads at the time of burning (Knicker, 2007). Moreover, grassland fires on slopes can move very quickly, so even when intense, the transfer of heat to the mineral soil is less damaging (Rollins et al., 1993). As a result, surface temperatures do not typically exceed 100 °C or 50 °C at 5 cm depth (Campbell et al., 1995). In addition, if the soils were dry at the time of burning, which is possible during the dry season, then belowground temperatures would rise very slowly because of the insulating properties of air-filled pores, which curtail heat transfer belowground (Neary et al., 1999). Although considerable C may have been lost at these lower temperatures, the organic matter can only be fully volatilized between 200 and 315 °C (Knicker, 2007). Grazing on the other hand, had a more negative impact on total SOC content than burning but there was not a significant loss. The exclusion of grazing has had mixed effects on total SOC in other studies, showing increases (Su et al., 2004; Steffens et al., 2008), decreases (Reeder and Schuman, 2002) or no change (McIntosh et al., 1997). The principal

explanations for the varying outcomes are grazing intensity and duration of grazing exclusion (Chen et al., 2012), and potentially in this study, the grazing pressure on these sites may have been below the threshold to cause severe degradation, which corroborates with a previous study based in the Peruvian Andes, where they also found no significant effect of grazing or burning on total SOC stocks (Gibbon et al., 2010).

Grazing appeared to negatively impact the free LF, but had little or no impact on total SOC. Grazing is known for reducing aboveground biomass (Johnson and Matchett, 2001; Gibbon et al., 2010), so a lower incorporation of detritus into the soil is not surprising. A reduction in labile C fractions has also been observed in other grazing studies, where they found that the labile fraction increased with grazing intensity, where by reducing the intensity of grazing, the labile fraction increased (Figueiredo et al., 2010). The effects of grazing on the free LF were most pronounced when grazing and burning occurred together, in which case, the free LF showed the most pronounced declines.

The occluded LF appeared to be more strongly affected by burning rather than grazing. Unburnt soils did not show significant differences in the occluded LF, whereas burnt soils tended to show a significant increase in the occluded LF. For example, when combining data from across different soil depths (0-30 cm), the grazed - burnt and non grazed - burnt soils had a much higher proportion of C in the occluded LF compared to the non-burnt soils. This may be the result of charcoal particles (from burning) becoming incorporated into the occluded LF. Charcoal, because of its low density, tends to reside in the lighter fractions (Cadisch et al., 1996; Sollins et al., 2006; Glaser et al., 2000), despite its recalcitrance. Because the fires took place almost ten years ago, the charcoal may no longer be residing in the free LF but may have become occluded into soil micro-aggregates due to its high sorptive capacity (Qayyum et al., 2014). Once incorporated into micro-aggregates, charcoal can be maintained for centuries after fire (Zackrisson et al., 1996).

Lastly, some of the differences in soil C fractions may be attributable to site-specific differences in microclimate or other environmental conditions. For example, when analysing the two montane grassland sites separately, the grazed-burnt plot at Wayqecha had significantly smaller proportions of free LF at 0-5

and 10-20 cm than Acjanaco. This pronounced land use effect may be a reflection of the warmer temperatures at Wayqecha (11.8 °C) compared to those at Acjanaco (6.8 °C).

No influence of burning on soil C stocks in upper montane forest

The effect of burning did not significantly alter total soil C content when the sites were combined, which is in keeping with another study in the same region, where no significant differences in C stocks were measured with the occurrence of low to moderate intensity fire (Gibbon et al., 2010). The most recently burnt site had no net change in soil C, which could have been a result of partly charred high C rich material mixing into the soil after a moderate fire (Knicker, 2007). The one exception to the rule is the Wayqecha (2003) site, where 50 % of soil C in the surface soil layer was lost. Greater soil C losses at Wayqecha (2003) may be due to the higher fire intensity at this plot, which caused substantial loss in aboveground biomass, slow vegetation recovery (which may have reduced subsequent SOM inputs into the soil), and a combination of accelerated erosion on these steep sided forests (McNabb and Swanson, 1990). This is consistent with other upper montane forests where fire severity is high (Román-Cuesta et al., 2011; Asbjornsen et al., 2005; Fearnside, 2000).

Agricultural abandonment in Premontane tropics increases soil C stocks

The impact of agricultural conversion on total soil C and soil C fractions was complex, with actual effects varying depending on land-use. The overall trend was a significant reduction in total SOC stocks down to 30 cm on the cultivated banana and low intensity grazed pasture soils compared to the mature forest (control), whereas the other land-uses did not vary significantly relative to the control. The proportion of free LF and heavy F C did not significantly vary among the cover types, with the exception of the cultivated banana soils, which had a significantly higher pool of occluded F and the pineapple with significantly lower free and occluded LFs than the others, suggesting that the baseline capacity for soil C storage is not affected by land management activities.

The mature forest, selectively logged forest and secondary forest had very similar total SOC stocks and density fractions down to 30 cm. This study had comparable SOC stocks (Telles et al., 2003; Dieleman et al., 2013; Zimmermann et al., 2010b) and density fractions to other studies (Marin-Spiotta et al., 2009;

Paul et al., 2008; Zimmermann and Bird, 2012) of the secondary forest SOC stocks has been seen in other tropical studies (Marín-Spiotta and Sharma, 2013) and is the result of rapid accumulations of organic matter that normally occur with secondary regrowth (Lugo and Brown, 1992; Post and Kwon, 2000).

The cultivated and abandoned banana sites were not significantly different to the mature forest in the first 0-5 or 5-10 cm, but the total SOC stocks down to 30 cm were significantly lower in the cultivated banana soils because of a significant loss in soil C at 10-20 cm. The cultivated banana soils had a significantly higher proportion of occluded LF to the control soils. This is an unexpected result as agricultural practices normally show a decrease in the free and occluded LFs (Piccolo et al., 2004; Wang and Wang, 2011). However, the losses of C appeared to come from the heavy F with both sites containing ~ 16 % less heavy F than the mature forest soils. The loss of SOC with agricultural plantation has been observed in many instances and is caused by limited vegetation input from crop residues and high disturbance (Schlesinger, 1986; Tiessen and Stewart, 1983). Studies on banana plantations are minimal but a study based in Costa Rica found that on multiple banana plantations, the total SOC content was reduced by 37 % (42 % for the cultivated banana in this study) in comparison to native forests and was explained by lower root biomass and leaf litter (Powers, 2004). Conversely, a study based in Brazil reported the opposite trend to this study, with a 14 % increase in total SOC in the top 10 cm, which was accounted for by larger proportions of heavy F compared to the native forest (Guimarães et al., 2013). However, in their study, fertilizers and organic residues were frequently added to the plantations, which can lead to up 66 % of the banana tree vegetation returned to the soil.

In the pineapple plantation soils there were no significant losses or gains in total SOC but the free and occluded LFs were significantly lower. The lower proportion of labile fractions may be related to the easily decomposable leaf material from pineapple plants. A decomposition study based in Malaysia measured a 90 % mass loss of pineapple leaf residue compared to only 30 % in sago plantations during a four month period (Nahrawi et al., 2011). The high total SOC content may be caused by the stabilisation of the heavy F, which may still have C present from the original forest before conversion to pineapple plantation and also the addition of new recalcitrant material from the trees present on the site.

The pasture soils in this study had no significant differences in total SOC or the three density fractions relative to the control in the surface soil layers (0-5 and 5-10 cm). However, the total SOC stocks on the low intensity grazed pasture was significantly lower when summing the depths down to 30 cm because of a significant loss in soil C at 10-30 cm. Discrepancies in C stocks are common on pasture soils, with studies reporting depletion (Veldkamp, 1994), increases (Trumbore et al., 1995) and no effect (Marín-Spiotta et al., 2008; Poeplau et al., 2011; Murty et al., 2002). This is partly due to land use history, but also because of the higher rates of belowground productivity from pastures, greater allocation to root biomass relative to trees and the influence of grazing (Elmore and Asner, 2006). The results from the intensively grazed site are surprising, as they had very similar total SOC stocks to the mature forest soils. In many studies, the influence of heavy grazing reduces the total SOC and labile fractions with the removal of fresh grass material (Elmore and Asner, 2006). However, when looking at the surface layers (0-5 and 5-10 cm), although not significant, this site had one of the lowest C concentrations compared to the other sites, whereas at 10-20 and 20-30 cm, there was a considerable increase in C content, which may have been caused by an increase in root turnover because of the regular removal of aboveground biomass and roots being a major source of SOC (Rasse et al., 2005).

The low intensity grazed pasture was highly enriched with pasture derived C (C4) in the total SOC and all three density fractions, which may have been due to a high abundance of grass detritus during times of recovery when the site was not grazed. The accumulation of C4 material in the heavier fractions could also be a reflection of site age, with the long historical presence of grasses causing the total SOC content to decrease. Despite this, the proportion of heavy F was still large and the loss of C from the total SOC probably came from the free LF, which was smaller compared to the other sites. The high soil CO_2 emissions and fast decomposition rates from this site support this theory (Chapter 3, Table 3.4 & Figure 3.4). Both the high intensity grazed and abandoned pasture soils had more C3-derived C compared to the low intensity grazed pasture. This may have been caused by a reduction of fresh grass material entering the soil on the high intensity grazed site or the presence of trees on the abandoned pasture contributing more recalcitrant material to the soil and the microbes preferentially degrading the grass material. Although not significant, these two sites had larger total SOC content than the low intensively grazed soils, which may have been the result of the greater proportion of forest derived C in the soil. Also, the C

in the heavy fraction on both of these sites was from forest material, which shows that the C still left from the forest after conversion to pasture is in a relatively passive state (Marin-Spiotta et al., 2009).

2.6 Conclusions

The results from this study have shown that land management can have varying degrees of influence on soil C storage and that the respective land management activities in lower elevations in the tropical Andes are more prone to soil C losses than those in the higher elevation ecosystems. It also emphasises how simply measuring total soil C stocks does not always give a true representation of how land management has affected soil C storage.

In the montane grasslands, total C stocks were unaffected by burning and grazing but a change in the distribution of soil C across physical density fractions were observed with significantly lower free LFs and burning alone, causing higher occluded LFs, due to the accumulation of black C. The upper montane forests had no significant net losses or gains from burning in the last 10 years. The one exception was a site where significant losses were measured in the surface soils, which may have been attributable to site-specific differences in micro climate or burning intensity. In the premontane elevation, the secondary forests and abandoned agricultural practices were similar to the mature forest in total SOC and density fractions. However, agricultural practices, such as the cultivated banana had significantly lower soil C stocks relative to the mature forest. The loss of C in these soils was not from the labile fraction as expected but rather from the more stable fractions. However, after eight years of abandonment and the presence of native trees, total soil C stocks appeared to recover. The total soil C stocks in the pasture soils were directly linked to the proportion of forest and grass derived C in the soil with the presence of trees increasing the proportion of forest derived material in all fractions and resulting in total C stocks similar to the mature forest. Whereas, the significant loss measured in the low intensity grazed pasture was probably the result of more easily decomposable grass material dominating the free LF.

When choosing sites for C sequestration projects, it is crucial that we have an understanding of the types of disturbance and land-use activities that disrupt or maintain a soil's capacity to physically protect and store C. This study contributes to improving our knowledge in predicting the fate of soil C storage with future human activities in the tropics.

~ Chapter 3 ~

Soil CO_2 flux from different land uses on an elevation gradient in the Peruvian Andes

Montane cloud forest after burning in the Peruvian Andes.

3.1 Abstract

Tropical soils play a critical role in regulating atmospheric CO_2 concentrations, but this delicate soil-atmospheric gas exchange is increasingly under threat from deforestation, land use change and climate change. The Andes are of particular interest because of their high C density and exposure to different land management approaches. This study seeks to improve the understanding of differences of soil CO_2 fluxes in managed tropical Andean lands over a 2600 m gradient, including: the effect of grazing and burning on high altitude montane grasslands; burning in the montane cloud forests; and the influence of agriculture in the premontane forests (abandoned and cultivated banana plantations, pasture, selective logging and secondary forest). In addition to comparing annual soil CO_2 fluxes, the main environmental drivers of soil respiration (soil moisture and temperature) were also examined along with decomposition rates of a common substrate buried at 10 cm, which was used as a proxy of heterotrophic respiration. Soil CO_2 fluxes were measured bi-monthly using a closed-chamber technique with a Vaisala CO_2 analyser, along with soil moisture, temperature and soil properties, such as: pH, total C content, bulk density and soil texture. There were large differences in soil CO_2 fluxes among the three elevations; 0.91 ± 0.06 μmol m^{-2} s^{-1} in the montane grasslands 1.50 ± 0.06 μmol m^{-2} s^{-1} in the cloud forest and 2.76 ± 0.30 μmol m^{-2} s^{-1} in the premontane forest. Overall, land management affected the magnitude and drivers of soil respiration and decomposition rates in the montane grasslands and premontane forest but not the upper montane cloud forest. In the high elevation montane grasslands, burning and grazing significantly increased soil respiration rates (1.35 ± 0.14 μmol m^{-2} s^{-1}) and the overall driver was temperature, but the temperature effect was diminished with the combined influence of burning and grazing. In the upper montane forest, burning did not significantly affect soil respiration rates (1.43 ± 0.06 μmol m^{-2} s^{-1}) and variances in fluxes were explained by time of year and air temperature, but there were only significant losses in total C at one of the sites. At the premontane elevation, pasture was the only land use to have a significant effect on soil respiration (6.24 ± 0.44 μmol m^{-2} s^{-1}) but the environmental drivers affecting fluxes were altered. The most influential driver on the agricultural land uses was soil temperature, as opposed to the well-established soil moisture content that affects tropical forest soils.

3.2 Introduction

Soil respiration is an integral part of the ecosystem carbon (C) cycle and plays a critical role in regulating atmospheric CO_2 concentrations by contributing more than 25 % of the total annual biogenic CO_2 emissions to the atmosphere (Raich and Schlesinger, 1992; Luo and Zhou, 2006; Raich et al., 2002). In particular, tropical and subtropical forest soils are one of the largest contributors to global soil respiration (Doff Sotta et al., 2004) with Amazonian soil CO_2 fluxes ranging from 3.2 to 6.2 µmol m^{-2} s^{-1} (Trumbore et al., 1995; Meir et al., 1996; Davidson et al., 2000b; Chambers et al., 2004). Over the last century, the global C cycle has been altered by increasing deforestation in the tropics and although it is difficult to determine how much of the global CO_2 emissions are from anthropogenic land use change (Le Quere et al., 2009), estimates are 1.1 ± 0.3 Gt C yr^{-1}, with 20 % of this budget from soil C loss (Achard et al., 2004).

Soil CO_2 fluxes from different land covers in the tropics are poorly understood, especially in terms of distinguishing alterations in the environmental drivers of soil respiration on multiple land-uses. Conversion to pasture and the succession of secondary forests are the predominant cover types studied in the tropics (Li et al., 2005; Pinto et al., 2006; Trumbore et al., 1995; Davidson et al., 2000a; Salimon and Davidson, 2008; Salimon et al., 2004). However, agricultural practices have received little attention, except a few studies on agroforestry sites (Bae et al., 2013; Mutuo et al., 2005) and a focus on oil palm and sago plantations in Malaysia, where no mean differences in soil CO_2 flux among sites were found but evidence suggested that soil respiration was affected by different environmental factors (Melling et al., 2014; Adachi et al., 2006; Melling et al., 2005). Similar findings were discovered in Southwest China, where soil temperature affected soil respiration on a mature forest and not on a rubber plantation (Werner et al., 2006). In order to estimate regional C budgets, a better understanding of the dominant drivers of soil respiration on multiple land uses is needed in tropical C cycling research (Ramankutty et al., 2007; Davidson et al., 2000b; Pendall et al., 2010).

The Peruvian tropical forests are the third largest in the world and have experienced rapid changes in land use between 1999 and 2007, with estimated annual deforestation rates of 645 km^2 yr^{-1} (Brooks et al., 2006; Oliveira et al., 2007) and annual gross aboveground C emissions of 4.5 Tg of C, as a result of land

use change between 1999 and 2000 (Asner et al., 2010). They cover a variety of ecosystems, ranging from high-altitudinal montane grassland, between the permanent snowline and the continuous montane cloud forest (Luteyn, 1992), down to premontane rainforest. These upland ecosystems (> 500 m a.s.l) account for almost 80 % of the total land cover in Peru (Feeley and Silman, 2010) and 8 % in South America (Eva et al., 2004). However, most land-use change studies have focused on lowland forests, with little emphasis on montane environments above 500 m a.s.l, particularly on belowground C stocks and land use change.

In high montane grasslands (> 3200 m a.s.l), cattle grazing has been a common and widespread practice since the 1500's (Balser and Wixon, 2009) and is sustained by pervasive burning to maintain high productivity of the forage grasses (Johansson et al., 2012; Luteyn, 1992; Sarmiento, 2002). To some extent, this natural system is tolerant of these management practices (Ramsay, 1992). However, in recent years, it has become apparent that the combination of global warming, which is causing drier conditions during intense El Nino events and the considerable pressure from agricultural expansion, have resulted in increased fire occurrence and downward in the cloud forest tree line (Cochrane and Ryan, 2009). Studies in montane grasslands have found that an increase in the frequency of fire events can reduce the amount of soil organic matter (SOM) in the top soil (Knicker, 2007) (Chapter 2, Table 2.2) or it may increase the biomass growth period afterwards, causing more detritus to accumulate in the upper soil layers (Ojima et al., 1994).

In the upper montane cloud forest (2200 – 2100 m a.s.l), studies in Southern Mexico and the Peruvian Andes have found that forest fires can cause an immediate reduction of 89 % soil organic C (Asbjornsen and Wickel, 2009; Román-Cuesta et al., 2011). The long term recovery of these soils and the associated soil respiration are unknown but the potential long term impact of fire damage could result in increased soil erosion (Imeson et al., 1992), reduction in water holding capacity, an increase in bulk density (Huffman et al., 2001) and a reduced canopy layer, all which may have a continued influence on soil CO_2 emissions.

In the premontane rainforest (600 – 1200 m a.s.l), deforestation is primarily influenced by timber production, agroecosystems and pastures, with 27 % of the forest loss due to selective logging and 68 % from agriculture between 1999 and 2005 (Asner et al., 2010). Conversely, there has also been an increase in successional forests (Wright, 2005) due to the widespread abandonment of agriculture (Aide and Grau, 2004; Lambin and Meyfroidt, 2011). The effects of land-use change on soil CO_2 efflux is contingent on the management practice applied. For example, conversion of forest to pasture can cause substantial soil disturbance initially due to the release of C from deeper soil layers as a result of mixing and the breakup of soil aggregates exposing previously inaccessible C for microbes (Post and Kwon, 2000), but there are disparate findings as to whether the higher proportion of below-ground biomass from the grasses increase CO_2 fluxes in the long term (Lugo and Brown, 1992; Guo and Gifford, 2002; Murty et al., 2002). Whereas, conversion of forest to arable crops or fruit cultivation (e.g. banana, soybean, maize, coffee, cocoa etc.) use either slash and burn or a slash and mulch system with organic material taken from forestry waste. This may initially produce very organic rich soils (Holland and Coleman, 1987) and higher yields (Rukazambuga et al., 2002) but as these organic residues decompose over several years, these soils may become nutrient poor if no additional fertilizers are applied. The process of selective logging can cause changes in the microclimate of a forest, erosion, soil compaction from the initial tree falling, increased fire susceptibility and disruption in nutrient cycles (Asner et al., 2004; McNabb et al., 1997), all of which may have an effect on soil respiration. After a period of time, all these systems establish a new equilibrium or steady-state (Poeplau and Don, 2013) but the long term change in the type and density of above and below ground biomass and the physical characteristics (Knicker, 2007) and biochemical processes of the soil can cause ongoing differences in the amount of CO_2 emitted among different land uses.

The quantification of soil CO_2 fluxes on a range of land uses in different ecosystems in the upland tropics is scarce. Additionally, there are uncertainties in how the environmental drivers (soil moisture and temperature) of soil respiration are affected. In order to improve our understanding of managed upland tropical ecosystems, we explored and compared the different controls on soil C fluxes from a representative number of different land uses on a broad scale elevation gradient in the Peruvian Andes. The specific objectives of this study were to:

1. Quantify differences in soil respiration among different land uses from three elevation bands;
2. Evaluate the role of environmental drivers among these land uses in regulating soil respiration fluxes, including factors such as: soil temperature, moisture, C content, texture, bulk density and rainfall events.

3.3 Methods

3.3.1 Site descriptions

The study region is based within the Manu Biosphere Reserve in the south-eastern Peruvian Andes. Different land uses were chosen from three distinctively different ecosystems along an elevation transect through the Koñsnipata Valley; ranging from high altitude montane grassland (3200 m a.s.l; colloquially referred to as 'Puna'), upper montane forest (2200 - 3200 m a.s.l) down to premontane tropical forest (500 - 1200 m a.s.l). Twenty of the twenty three sites from the previous chapter were sampled for this soil respiration study. The three sites that were not included were: the pineapple (VC - PA), abandoned pasture (VC - P2) and intensively grazed pasture (VC - P1) from the premontane elevation. Detailed descriptions of the sites can be found in chapter 2 (2.3.1 Site descriptions) and a summary of site history for the 20 sites can be found in Table 3.1.

In the montane grassland, the effect of burning and grazing on CO_2 fluxes were investigated on two pre-established sites (July-August 2010) (Oliveras et al., 2014). This included two sites that were identified as being burnt in 2003 (Wayqecha) and 2005 (Acjanaco). In the tropical montane cloud forest, sites were chosen near the boundary between the cloud forest treeline and puna, where the presence of burning was likely the result of montane grassland fires spreading into the cloud forest. Three sites, with different burning years were chosen: Wayqecha in 2003, Acjanaco in 2005 and Sunchubamba in 2010.

In the premontane forest, six land uses were chosen: abandoned banana (V - AB); cultivated banana (V - B); mature forest (V - F); low intensity grazed pasture (V - P); selectively logged forest (V - SL) and secondary forest (V - SF). The abandoned banana site was abandoned in 2003 and now has the appearance of a forest and the currently cultivated banana site has been active for the last five years. The secondary forest site was cleared and transformed into a rice plantation more than twenty five years ago, and abandoned fifteen years ago. The selectively logged forest never ceased to be a forest but has a more open canopy. The pasture site was cleared more than twenty five years ago and has been used intermittently for intense periods of cattle grazing (3 months at a time), which stopped at the beginning of this experiment.

Table 3.1 Site and soil description for all twenty sites in the montane grassland, tropical montane cloud forest and premontane rainforest

Ecosystem	Site code	Site name	Dominant vegetation	Site history	Elevation (m a.s.l)	Annual precip. (mm)	Mean Temp. (° C)
Montane grassland	WP - BG	Wayqecha puna grazed-burnt	*Calamagrostis longearistata;*	Burnt in 2005	3121	1560	11.8
	W P- GNB	Wayqecha puna grazed- non burnt	*Scirpus rigidus;*	No burning			
	WP - NGB	Wayqecha puna non grazed-burnt	*Festuca dolichophylla*	Burnt in 2005			
	WP - NBNG	Wayqecha puna non grazed- non burnt		No burning			
	AP - BG	Acjanaco puna grazed-burnt		Burnt in 2003	3400	760	6.8
	AP - GNB	Acjanaco puna grazed- non burnt		No burning			
	AP - NGB	Acjanaco puna non grazed-burnt		Burnt in 2003			
	AP - NBNG	Acjanaco puna non grazed- non burnt		No burning			
Montane cloud forest	W - B	Wayqecha - burnt	*Weinmannia*	Burnt in 2003	3025	1710	12.5
	W - NB	Wayqecha - non burnt	*crassifolia;*	No burning			
	A - B	Acjanaco - burnt	*Clusia*	Burnt in 2005	3400		
	A - NB	Acjanaco - non burnt	*flaviflora;*	No burning			
	S - B	Sunchubamba - burnt	*Clusia alata*	Burnt in 2010	3200		
	S - NB	Sunchubamba - non burnt		No burning			
Premontane rainforest	V - F	Mature forest	*Precatoria; Guaduinae*	No signs of disturbance	580	4500	22
	V - SL	Selectively logged forest	*Socratea exorrhiza; Guadu: Iriartea deltoid*	Never ceased to be a forest	541		
	V - SF	Secondary forest		Abandoned rice plantation 25 years ago	565		
	V - P	Pasture (low intensity grazed)	*Poaceae Brachiaria*	Intense periods of cattle grazing	508		
	V - B	Banana cultivation	*Musa paradisiaca*	Slash and mulch - no burning or fertilizer	527		
	V - AB	Abandoned banana		8 years ago - no burning or fertilizer history	521		

Dominant vegetation for the puna and upper montane cloud forest were taken from (Oliveras et al., 2014) and for premontane land uses the vegetation was recorded by Adrian Tejedor (a full list species can be found in Appendix 1.1, Table 1.1)

3.3.2 Sample design

Different experimental designs were applied to the montane grassland, montane cloud forest and premontane rainforest and for the purpose of statistical analysis the elevation bands are reported separately. The sites in the montane grassland were set up in a factorial design, with burnt and adjacent non burnt plots (no more than 0.3 km apart), which were then split into two subplots; one with fencing constructed to stop cattle grazing and one left unfenced. Each site therefore had: a burnt- non grazed; burnt – grazed; non burnt - grazed and non burnt - non grazed plot. In the montane cloud forest, each burnt plot had a paired non burnt plot for comparison (no more than 30 metres away) and in the premontane forest, the different land uses were compared to each other and to the mature forest control plot. The sites were within 5 miles of each other apart from the mature forest which was approximately 16 km away from the agricultural plots (Chapter 2, Section 2.3.1).

On each land use, a 30 x 30 m plot was marked out and five permanent PVC chamber bases (diameter 20 cm, height 10 cm) were deployed randomly for the measurement of soil surface CO_2 fluxes, which took place morning and afternoon at two monthly intervals from July 2011 to July 2012. The chamber bases (total of 120 across all three elevations), were permanently inserted into the soil month prior to the first CO_2 flux measurements to allow the soil to settle and regrowth of vegetation inside the chambers bases was cut prior to measurement.

3.3.3 Soil respiration and environmental measurements

Soil respiration measurements were quantified using a static flux chamber technique with a Vaisala CARBOCAP® carbon dioxide probe and temperature sensor fitted inside a PVC cylindrical chamber (diameter 20 cm, height 20 cm), covered with a gas tight lid. The rate of CO_2 accumulation was measured every 30 seconds for 3 minutes by placing the chamber on the fixed chamber base with a gas tight rubber seal. Simultaneously, air temperature and atmospheric pressure were measured, using a type K thermocouple (Omega Engineering Ltd., UK) and Garmin GPSmap 60CSx (Garmin Ltd., USA).

Flux rates were calculated in R 3.0.2 (R_Core_Team, 2012) using the *HMR* package (Pedersen et al., 2010) by plotting the headspace concentration (ppm) against time (minutes) for each collar, which gave a

linear or non-linear regression, depending on the best fit. The Ideal Gas Law was then used to convert gas concentrations to moles of gas using the following equation:

$$n = PV/RT \quad \text{[Eq. 1]}$$

where n is the number of moles of CO_2 gas (mol), P is atmospheric pressure (atm), V is the volume (L), R is the idea gas constant (0.08205 L atm $°K^{-1}$ mol^{-1}), and T is temperature (K) (Livingston and Hutchinson, 1995). Fluxes were then reported in µmol m^{-2} s^{-1} and annual emissions were estimated by extrapolating each bi-monthly measurement to a 60 day period and summing for a year.

In addition, soil temperature (at 5 cm and 10 cm depth) and soil moisture (at 10 cm depth) were simultaneously measured in three locations adjacent to the collars using a ML2x ThetaProbe equipped with 12 cm rods (Delta-T Ltd., UK) and type K thermocouples (Omega Engineering Ltd., Manchester, UK) (Goldstein et al., 2000).

3.3.4 Soil sampling and analysis

Soil sampling: Soil samples were taken during the dry season in July 2012 with six replicates at 0-5, 5-10, 10-20 and 20-30 cm depths on each site and then further sampling with one replicate every 10 cm down to a metre in the premontane forest sites. Sampling was achieved by digging six pits randomly on each site and taking approximately 50 g of soil from each depth. Soil samples were air-dried and sieved with a 2 mm mesh sieve before being shipped to the University of St Andrews for all further analysis

Bulk density: Soil bulk density was determined by the soil core method (Black and Hartge, 1986). Undisturbed soil cores (30 cm^3) were taken in triplicate at 0-10, 10-20 and 20-30 cm. The samples were dried at 105 °C for 48 hours and bulk density was estimated as the mass of oven-dry soil divided by the core volume. Bulk density for the upper montane cloud forest and puna soils were taken from (Oliveras et al., 2014).

Carbon analysis: Soils were ground and homogenised using a grinding mill (Planetary Mono Mill PULVERISETTE) in preparation for C analysis at the University of St Andrews laboratories using a Finnegan Delta plus XP gas source mass spectrometer coupled to a Costech elemental analyser (EA-IRMS). Every ten samples, a duplicate sample was run with a replicate error < 5%. Classified standards were used (B2176, B2151, B2153 and sucrose). Total soil C was calculated as follows:

$$SOC = BD \times C\ content \times D \qquad [Eq.\ 2]$$

Where SOC is the soil organic carbon content (Mg ha^{-1}), BD is soil bulk density (Mg m^{-3}), C is the soil carbon content (g C kg^{-1}) and D is the soil sampling depth (m). (Hairiah et al., 1995; Brown, 1982).

Soil pH: Soil was collected at 0-5, 5-10, 10-20 and 20-30 cm depth in three replicates from all the sites and brought back to the laboratory for pH analysis. Soil pH was measured after shaking a 1:1 soil:deionized water ratio for the premontane rain forest soils and a 1:2 soil:deionized water for the cloud forest and montane grassland soils in suspension for 5 minutes (McLean, 1982).

Soil particle size: The distribution of soil particle size was measured in triplicate for each site at 0-5, 5-10, 10-20 and 20-30 cm depth by laser diffraction using a Beckman Coulter LS230 with a 70 nm diode laser, which had a size range of 400 nm to 2 mm and recorded on a 126 photodiode detector. Soils were air dried and sieved in a 2 mm sieve prior to analysis.

3.3.5 Decomposition experiment

A decomposition experiment was set up as an additional estimate of soil organic matter mineralisation and consisted of using birch wood sticks as a common substrate. Five sticks were placed in a mesh bag with three 2 cm holes cut into each bag to allow accessibility for both microfauna and fauna. In July 2011, eighteen bags were buried at 10 cm depth, in close proximity, on each site and three bags collected every two months. The sticks were weighed before the experiment started and again after collection, once they were air dried, to determine mass loss. The rate of decomposition was then calculated from the slope of a linear regression with time against mass loss.

3.3.6 Weather data

Daily precipitation and temperature data were taken between July 2011 and June 2012 from two weather stations: Chontachaka located at 982 m a.s.l was the nearest station to the sites at Villa Carmen and Pumataki at 3000 m a.s.l was used for the puna and upper montane cloud forest sites at Acjananco.

3.3.7 Statistical analysis

The three regions were analysed separately due to the confounding statistical effects that might occur due to the differing climates, soils and varying vegetation types along the elevation gradient. Statistical analyses were conducted in R version 3.0.2 (R Core Team, 2012). Outliers, likely due to instrumental or human error, were observed by visual inspection of the boxplots where points outside of the hinges (third quartile) were removed (only 5 out of 2156 data points were removed). The data were checked for normal distributions using histograms, QQ plots and the Shapiro-Wilk test. The CO_2 flux and volumetric water content (VWC) data were not normally distributed and therefore log transformed prior to parametric statistical analysis. Variables were also tested for collinearity and principal component analysis (PCA) was performed using the *'ggbiplot'* package (Wickham, 2009) to visually identify any correlations between the environmental data and CO_2 fluxes. Linear mixed effect models were conducted to identify any relationships between the environmental variables and soil characteristics with soil CO_2 fluxes for each site, individually. This takes into account the random effect of multiple measurements taken on the same collar throughout the year, which would otherwise violate the independence assumption. In this respect, mixed model restricted maximum likelihood analysis (REML) were computed using the *lme4* package (Bates et al., 2014) to include random intercepts for each collar. Soil temperature (5 cm), volumetric water content (VWC), season, time of day, site and month were entered as fixed effects in the model and collar as a random effect, as well as by-month random slopes for the effect of soil CO_2 flux. The experimental design in the montane grassland was factorial, with the effect of grazing nested within the burnt sites and so the model was altered to include grazing as a random effect. Model selection and significance (reported at $p < 0.05$) was obtained by using likelihood ratios and Akaike information criterion (AIC) of the full model with the effect in question against the model without the effect in question. Residuals were visually assessed for large deviations from assumptions of homogeneity and

normality (Zuur et al., 2009). Analysis of variance (ANOVA) and Tukey's Honest Significant Different (HSD) post hoc test were used to examine statistically significant differences between means of the environmental data among the sites. Linear regression analysis was used on the decomposition data to examine the relationship between the dry weight remaining of the common substrate with time for each site and then tested to identify any relationships with the soil CO_2 fluxes.

3.4 Results

3.4.1 Soil respiration among different land uses from three elevation gradients

Grazing and burning in high elevation montane grasslands

The combination of grazing and burning significantly increased soil CO_2 fluxes in the montane grasslands. However, this was more noticeable at Wayqecha (2003) than at Acjanaco (2005). Regardless of land use, the plots at Wayqecha (2003) had greater variability and overall higher annual mean soil temperature (15 °C) and CO_2 flux (1.34 ± 0.09 µmol m^{-2} s^{-1}) compared to the sites in Acjanaco (2005) (12 °C and 0.79 ± 0.03 µmol m^{-2} s^{-1}) (Table 3.2). The highest measured temperatures and CO_2 fluxes at Wayqecha were synchronously recorded during July-11, November-12 and March-1 (Figure 3.1), whereas at Acjanaco the changes in CO_2 flux with season and temperature were less detectable. Land use did not alter the pH (~ 4.5) and there were no significant differences in soil C content among the sites or between grazing (p-value = 0.44) and burning (p-value = 0.70) when the sites were combined.

Table 3.2 Annual and seasonal mean soil temperature, VWC and CO_2 flux for Wayqecha and Acjanaco in the montane grassland.

Site / land use / season	Soil temp. (°C) at 5 cm	VWC (%) at 5 cm	CO_2 flux (µmol m^{-2} s^{-1})	Annual CO_2 emission (Kg C m^{-2} yr^{-1})	pH 0-5 cm	Soil C 0-5 cm (Mg C ha^{-1})
Wayqecha (2003)	14.7 ± 0.1	62.3 ± 0.4	1.31 ± 0.09	0.49		
Grazed – burnt	15.3 ± 0.3^{a}	63.4 ± 0.3^{ab}	1.88 ± 0.23^{a}	0.40	4.3 ± 0.1^{a}	40.0 ± 1.3^{a}
Grazed - non burnt	14.5 ± 0.2^{ab}	63.8 ± 0.2^{ab}	1.07 ± 0.07^{b}	0.38	4.3 ± 0.1^{a}	41.3 ± 8.9^{a}
Non grazed - burnt	14.6 ± 0.3^{ab}	60.9 ± 1.0^{c}	0.99 ± 0.08^{bc}	0.41	4.1 ± 0.0^{a}	40.3 ± 2.6^{a}
Non grazed - non burnt	14.1 ± 0.2^{b}	62.5 ± 0.8^{bc}	1.10 ± 0.07^{ab}	0.31	4.6 ± 0.0^{a}	38.7 ± 4.1^{a}
Dry season	14.1 ± 0.2	61.4 ± 0.8	1.35 ± 0.16			
Wet season	15.1 ± 0.20	63.8 ± 0.3	1.31 ± 0.10			
Minimum	11.6	29.9	0.22			
Maximum	18.0	65.8	8.33			
Acjanaco (2005)	11.6 ± 0.1	64. 5 ± 0.1	0.91 ± 0.03	0.29		
Grazed - burnt	12.0 ± 0.2^{c}	64.0 ± 0.2^{ab}	0.82 ± 0.05^{bc}	0.31	4.7 ± 0.1^{a}	40.2 ± 5.0^{a}
Grazed – non burnt	11.5 ± 0.2^{cd}	64.5 ± 0.2^{ab}	0.84 ± 0.07^{bc}	0.31	4.2 ± 0.0^{a}	41.4 ± 2.4^{a}
Non grazed - burnt	11.9 ± 0.1^{cd}	64.2 ± 0.2^{ab}	0.77 ± 0.05^{c}	0.29	4.6 ± 0.1^{a}	53.5 ± 3.5^{a}
Non grazed - non burnt	10.8 ± 0.1^{d}	65.1 ± 0.2^{a}	0.72 ± 0.05^{c}	0.27	5.1 ± 0.1^{a}	48.0 ± 1.3^{a}
Dry season	11.6 ± 0.1	63.8 ± 0.2	0.81 ± 0.04			
Wet season	11.7 ± 0.1	65.1 ± 0.1	0.74 ± 0.03			
Minimum	9.5	57.1	0.09			
Maximum	13.7	67.7	2.69			
GRAZED – BURNT	13.8 ± 0.2^{a}	63.7 ± 0.2^{a}	1.35 ± 0.13^{a}	0.51		
GRAZED – NON BURNT	13.2 ± 0.2^{a}	64.1 ± 0.1^{a}	0.95 ± 0.05^{b}	0.36		
NON GRAZED – BURNT	13.3 ± 0.2^{a}	62.6 ± 0.5^{a}	0.88 ± 0.05^{b}	0.33		
NON GRAZED – NON BURNT	12.6 ± 0.2^{a}	63.8 ± 0.4^{a}	0.91 ± 0.05^{b}	0.35		

Different letters down the columns represent significant differences between sites. Soil C and pH values are given with 1 standard deviation of the mean (n = 3).

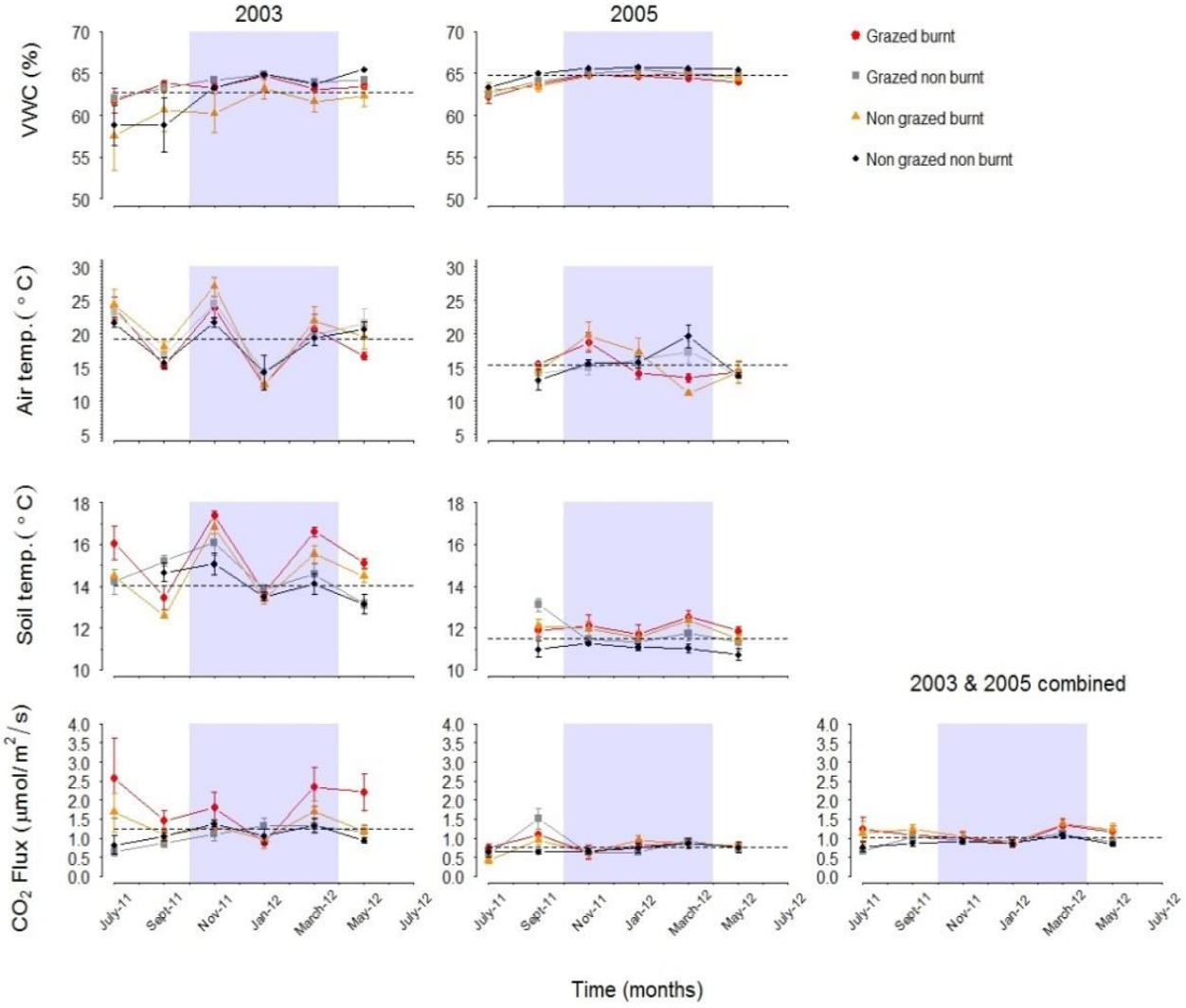


Figure 3.1 Monthly soil temperature (5 cm), air temperature, soil VWC (0-10 cm) and soil CO_2 flux from grazed and non-grazed subplots on sites burned in 2003 (Wayqecha) and 2005 (Acjanaco) and adjacent non burnt sites in the montane grassland. The graph on the right represents the mean CO_2 flux of both burnt sites combined. For CO_2 fluxes, each symbol is a mean of 4 chambers with morning and afternoon measurements combined and standard errors (n = 8) are plotted as error bars. The dotted line represents the mean for that site and the blue band represents the wet season (Oct-March).

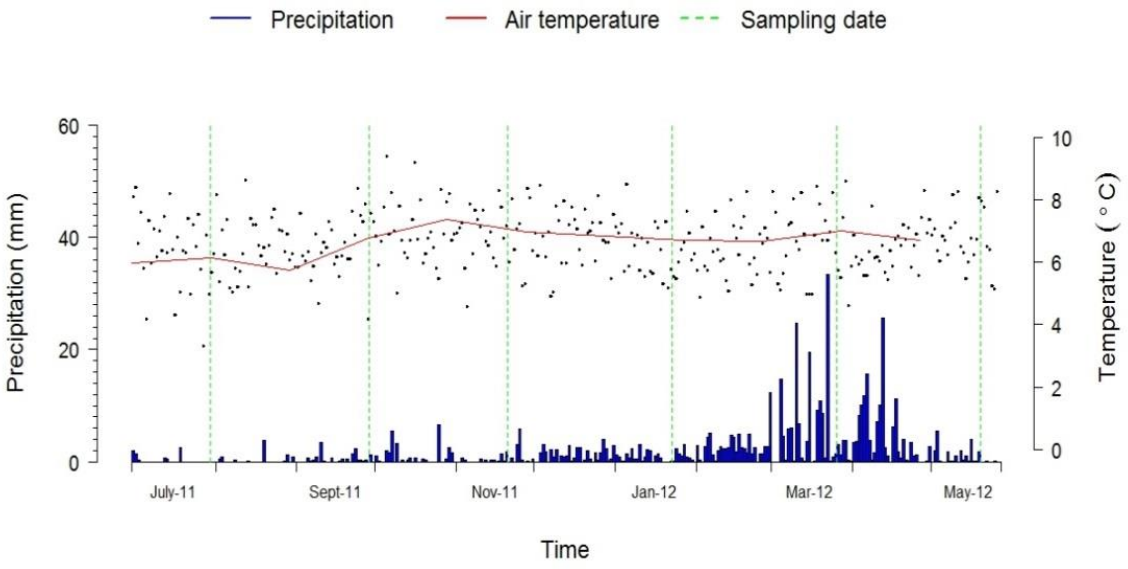


Figure 3.2 Daily precipitation (mm) and temperature (°C) data for the high elevation montane grassland between July 2011 and June 2012.

Daily precipitation and air temperature data are illustrated in Figure 3.2 with the sampling days highlighted. During this experiment there was 358 mm of rain in the wet season (October – March) and 187 mm in the dry season (April – September). Weather data for the plots at Wayqecha were unavailable but similar rainfall events will have occurred in the two areas due to their close proximity. In January 2012, there was no precipitation for at least a week prior to sampling, which may have resulted in lower CO_2 flux measurements recorded for that month. The reverse of this was seen in March 2012, which had a large increase in fluxes at Wayqecha and some of the highest rainfall events of the year, with more than 30 mm of rainfall in the days prior to sampling (Figure 3.1). However, this is speculative and more sampling dates would be required to ascertain any relationships between precipitation and CO_2 fluxes.

Burning in upper montane cloud forests

There was no significant effect of burning on soil CO_2 fluxes in the cloud forest. Across all the sites, there was approximately a 20 % increase in fluxes from the dry season to the wet season. There were also no significant difference among the three areas measured but the sites at Wayqecha were on average higher than the others sites. Soil and air temperatures did not fluctuate between seasons but there were erratic

deviations throughout the year and slightly higher temperatures occurring on the burnt plots on all three sites. On average, temperatures were lower at Acjanaco and the single high temperature measured in July 2011 (16 °C) at Sunchubamba was most likely due to sampling taking place two days after the fire occurred. A seasonal trend could be seen with soil VWC, with a wide range of measurements recorded (1.6 – 64 %) or 18 to 64 % if you exclude the values recorded during the same month as the fire. Soil VWC was 20 % higher at Acjanaco than at the other sites and consistently high throughout the year and across all the sites, the burnt plots were also marginally wetter (Figure 3.3). The burnt plot at Wayqecha was significantly more alkaline and soil C at 0-5 and 10-20 cm was significantly higher on the non - burnt plots ($p = 0.01$) (Table 3.3).

Table 3.3 Annual and seasonal mean soil temperature, VWC, CO_2 flux and soil properties for burnt and adjacent non burnt plots at Wayqecha, Acjanaco and Sunchubamba in the montane forest.

Land use	**Site / season**	**Soil temp. (°C) at 5 cm**	**VWC (%) at 5 cm**	**CO_2 flux (µmol m^{-2} s^{-1})**	**Annual CO_2 emission (Kg C m^{-2} yr^{-1})**	**pH 0-5 cm**	**Soil C 0-5 cm (Mg C ha^{-1})**
Burnt	Sites combined	11.7 ± 0.2	45.9 ± 1.2	1.43 ± 0.06	0.54		
	Dry season	11.5 ± 0.3	39.7 ± 1.8	1.29 ± 0.07			
	Wet season	10.6 ± 0.2	52.1 ± 1.1	1.56 ± 0.08			
	Minimum	8.1	1.6	0.24			
	Maximum	20	66.0	6.01			
	Wayqecha (2003)	12.5 ± 0.2^{a}	39.8 ± 1.4^{b}	1.46 ± 0.11^{a}	0.55	4.2 ± 0.2^{b}	3.0 ± 1.4^{a}
	Acjanaco (2005)	9.9 ± 0.1^{c}	58.5 ± 1.5^{a}	1.42 ± 0.08^{a}	0.54	4.9 ± 0.2^{a}	5.5 ± 1.7^{a}
	Sunchubamba (2010)	12.5 ± 0.2^{a}	39.4 ± 2.0^{b}	1.40 ± 0.11^{a}	0.53	3.5 ± 0.2^{c}	7.4 ± 1.1^{b}
Non Burnt	Sites combined	10.5 ± 0.1	38.7 ± 1.3	1.50 ± 0.06	0.56		
	Dry season	11.8 ± 0.2	30.2 ± 1.7	1.41 ± 0.10			
	Wet season	10.6 ± 0.1	48. 7 ± 1.0	1.60 ± 0.06			
	Minimum	7.6	3.4	0.12			
	Maximum	13.8	64.4	5.59			
	Wayqecha	11.0 ± 0.1^{b}	37.4 ± 1.7^{b}	1.66 ± 0.11^{a}	0.63	3.3 ± 0.1^{c}	6.0 ± 1.3^{a}
	Acjanaco	8.8 ± 0.2^{d}	49.9 ± 4.4^{a}	1.31 ± 0.08^{a}	0.50	4.3 ±0.1^{ab}	6.5 ± 1.7^{a}
	Sunchubamba	10.6 ± 0.1^{bc}	36.4 ± 1.9^{b}	1.49 ± 0.07^{a}	0.56	3.3 ± 0.1^{c}	7.6 ± 0.6^{b}

Different letters down the columns represent significant differences between sites. Soil C and pH values are given with 1 standard deviation ($n = 3$).

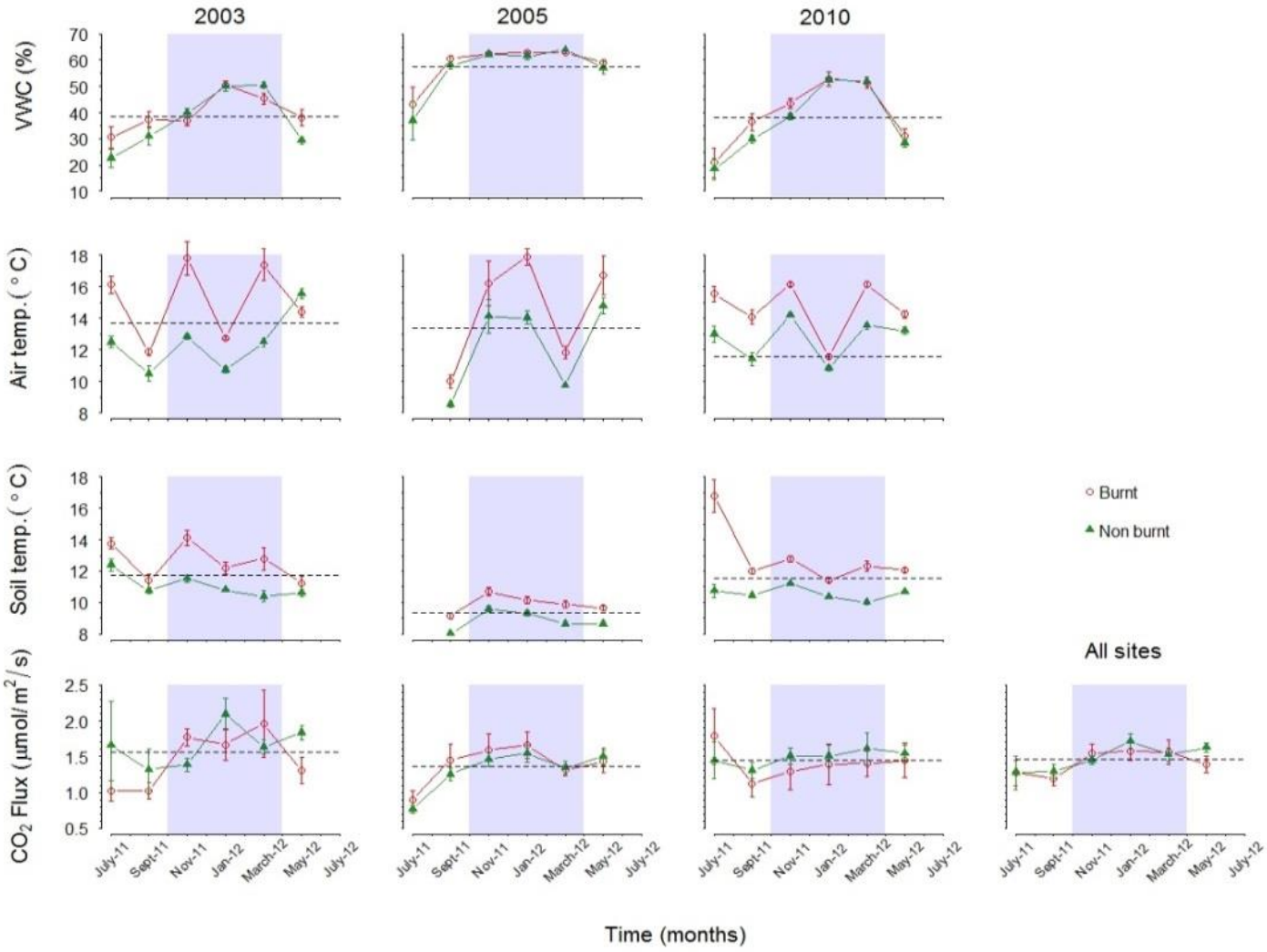


Figure 3.3 Monthly soil temperature (0-5 cm), air temperature, soil volumetric water content (0-10 cm) and emissions of CO_2 from three burnt sites and adjacent non-burnt sites in the montane forest. From left to right are the observations from the site burnt in 2003 (Wayqecha), 2005 (Acjanaco), 2010 (Sunchubamba) and all the sites combined. For CO_2 fluxes, each symbol is a mean of 5 chambers with morning and afternoon measurements combined and standard errors of the mean are plotted as error bars (n = 10). The dotted line represents the mean for that site and the blue band represents the wet season (Oct-March).

Agricultural land uses in premontane forests

Pasture was the only land use to show a significantly higher rate of soil respiration relative to the control (i.e. mature forest) in the premontane elevation band. The pasture soils showed the highest mean annual soil CO_2 fluxes (6.24 ± 0.44 µmol m^{-2} s^{-1}) compared to the other land uses and had the largest spatial variability as well as broadest range of fluxes (Figure 3.4). Whereas, the mature forest, abandoned banana, cultivated banana, secondary forest and selectively logged sites had similar annual mean soil respiration rates, averaging at 2.98 ± 1.14 µmol m^{-2} s^{-1}. The CO_2 fluxes on the abandoned banana site had the largest increase from dry to wet season (2.97 ± 0.26 to 4.14 ± 0.26 µmol m^{-2} s^{-1}), whereas for the other sites, there was minimal change with season. The initial high fluxes measured on the secondary forest and selectively logged forest in July 2011 may be due to the initial disturbance of the soil after the collars were installed (Table 3.4).

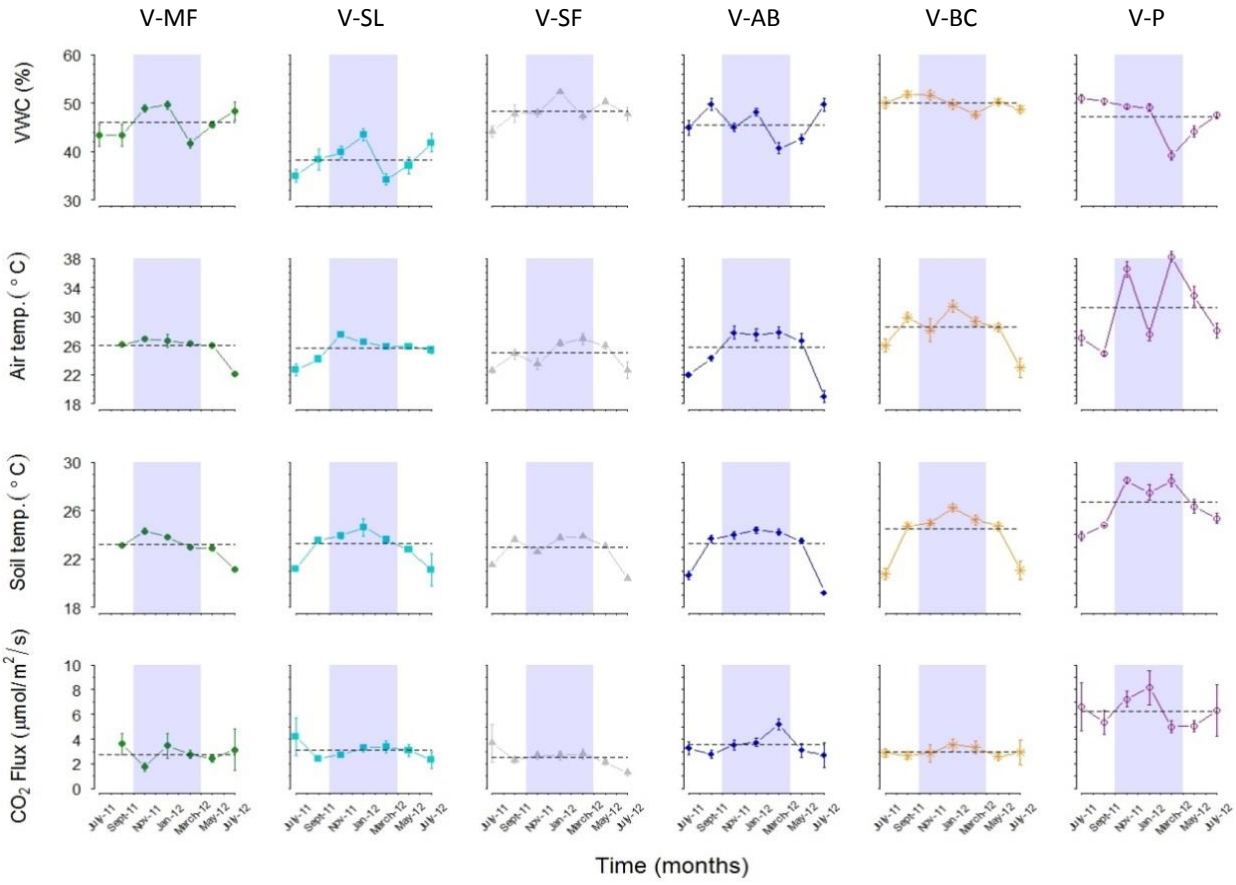


Figure 3.4 Monthly soil temperature (0-5 cm), volumetric water content (0-10 cm) and emissions of CO_2 from soils of six land uses in the premontane elevation. For CO_2 fluxes, each symbol is a mean of 5 chambers with morning and afternoon measurements combined (10 measurements per month) and 1 standard error of the means are plotted as error bars (n = 10). The blue band represents the wet season (Oct – April).

The selectively logged forest had the lowest annual mean soil VWC (39 %), whilst the highest was measured on the cultivated banana (50 %). In January 2012 there was an increase in soil VWC on all the sites, apart from the pasture and cultivated banana soils, which were already high. This coincided with heavy rains on the day of sampling (63 mm) (Figure 3.5). The low soil VWC measured on all the sites in March 2012 also observed the same pattern with a few drier days prior to sampling. Mean annual soil temperature at 10 cm depth was similar on all the sites, apart from the pasture (27 °C) and cultivated banana (25 °C) sites, which were statistically higher. Among all the sites, soil temperature increased by a maximum of 3 °C from the dry to the wet season and was relatively stable on the mature forest, selectively logged and secondary forest, throughout the year. Whereas, on the pasture, abandoned banana and cultivated banana sites, the range was much greater, with the highest temperatures in the wet season.

Soil pH was similar across all the sites, averaging at ~ pH 5 and although there were no significant differences in bulk density, the secondary forest had the highest (0.46 ± 0.02 g cm^{-3}), with the lowest occurring on the selectively logged soils (0.32 ± 0.06 g cm^{-3}). Soil particle size distribution determined that the mature forest, pasture, and selectively logged forest were sandy loams and the secondary forest, abandoned banana and cultivated banana were silty loams. There were no significant differences in total C content among the land uses. However, the cultivated banana and pasture soils had the lowest total C content (16.3 ± 0.5 and 19.7 ± 1.7 Mg C ha^{-1}, respectively) and the highest was measured in the mature forest soils (28.4 ± 2.4 Mg C ha^{-1}) (pasture soils here refer to low intensity grazed (VC-P) in Chapter 2, Table 2.1).

Illustrated in figure 3.7, the sampling days are highlighted with the daily precipitation and air temperature data. The total rainfall for 2012 was 4570 mm, which was slightly lower than previous years (2011 = 5580 mm, 2010 = 5310 mm, 2009 = 5530 mm). During this experiment there was 3026 mm of rain in the wet season (October – March) and 1865 mm in the dry season.

Table 3.4 Significant relationships between CO_2 efflux and the environmental data in the premontane elevation.

Site	Soil temp. (°C) at 5 cm	VWC (%) at 5 cm	CO_2 flux (µmol m^{-2} s^{-1})	Annual CO_2 emission (Kg C m^{-2} yr^{-1})	pH 0-5 cm	Bulk density (g cm^{-3}) 0-10 cm	Texture 0-10 cm	Soil C 0-5 cm (Mg Cha^{-1})
V - MF	23.2 ± 0.2^{c}	46.1 ± 0.6^{bc}	2.76 ± 0.30^{c}	1.05	5.1 ± 0.1^{a}	0.43 ± 0.05^{a}	60/36/4	7.4 ± 1.2^{a}
Minimum	20.9	36.9	0.43					
Maximum	26.1	54.7	11.11					
Dry season	22.5 ± 1.0	45.3 ± 0.8	2.91 ± 0.47					
Wet season	23.7 ± 0.2	46.8 ± 0.8	2.66 ± 0.39					
V - SL	23.3 ± 0.2^{c}	38.3 ± 0.7^{d}	3.12 ± 0.27^{bc}	1.18	5.4 ± 0.1^{a}	0.32 ± 0.06^{a}	74/24/2	6.6 ± 1.3^{a}
Minimum	15.8	28.2	0.65					
Maximum	31.0	50.4	13.12					
Dry season	22.5 ± 0.3	37.67 ± 1.0	3.09 ± 0.47					
Wet season	24.0 ± 0.3	39.2 ± 1.0	3.13 ± 0.20					
V - SF	23.0 ± 0.2^{c}	48.3 ± 0.5^{ab}	2.51 ± 0.17^{c}	1.09	5.5 ± 0.2^{a}	0.46 ± 0.02^{a}	31/64/5	6.7 ± 0.6^{a}
Minimum	20.1	37.1	0.64					
Maximum	25.2	54.2	9.72					
Dry season	22.5± 0.3	47.5 ± 0.8	2.31 ± 0.29					
Wet season	23.4 ± 0.2	49.2 ± 0.5	2.71 ± 0.19					
V - AB	23.3 ± 0.2^{c}	45.6 ± 0.6^{c}	3.54 ± 0.20^{b}	1.34	5.7 ± 0.2^{a}	0.33 ± 0.04^{a}	62/36/3	6.4 ± 1.3^{a}
Minimum	18.9	36.2	0.24					
Maximum	25.9	55.2	7.67					
Dry season	22.4 ± 0.4	46.4 ± 0.8	2.97 ± 0.26					
Wet season	24.2 ± 0.2	44.6 ± 0.8	4.15 ± 0.26					
V - B	24.5 ± 0^{b}	50.1 ± 0.4^{a}	2.98 ± 0.20^{bc}	1.14	5.3 ± 0.2^{a}	0.44 ± 0.02^{a}	24/71/4	4.6 ± 0.6^{a}
Minimum	18.4	42.1	0.73					
Maximum	28.0	55.4	7.68					
Dry season	23.5 ± 0.48	50. 5 ± 0. 5	2.72 ± 0.22					
Wet season	25.5 ± 0.2	49.7 ± 0.6	3.24 ± 0.32					
V - P	26.7 ± 0.3^{a}	47.2 ± 0.6^{bc}	6.24 ± 0.44^{a}	2.38	5.6 ± 0.0^{a}	0.41 ± 0.01^{a}	46/51/3	4.8 ± 0.8^{a}
Minimum	22.5	35.9	1.17					
Maximum	30.6	54.9	17.01					
Dry season	25.4 ± 0.3	48.4 ± 0.7	5.75 ± 0.65					
Wet season	28.2 ± 0.3	45.9 ± 1.0	6.80 ± 0.57					

Different letters down the columns represent significant differences between sites. Bulk density, soil pH and C values are given with 1 standard deviation (n = 3). Soil texture represents proportions (%) of sand/silt/clay. Significant code * = P< 0.05.

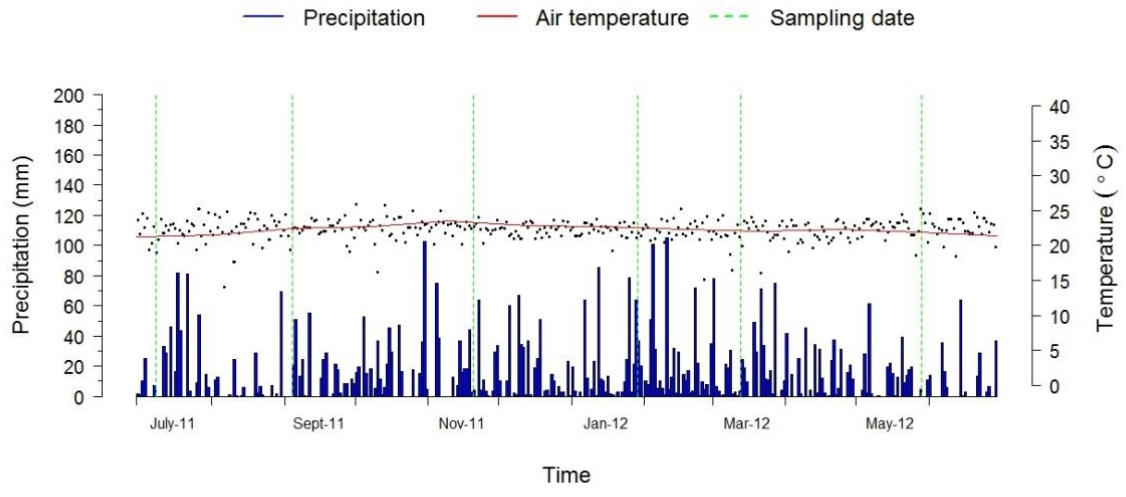


Figure 3.5 Daily precipitation (mm) and temperature (°C) data for the premontane forest between July 2011 and June 2012.

3.4.2 Environmental drivers of soil respiration among the different lands uses and elevation gradients

In the montane grassland, season, soil and air temperature were the main drivers of soil respiration (p-values = 0.031, 9.3 x 10^{-7} and 0.0001, respectively), with higher temperatures having a positive effect on soil CO_2 fluxes. However, land-use specific differences were observed on the grazed-burnt plots at both Wayqecha and Acjanaco, with no significant relationships between soils CO_2 fluxes and environmental variables measured (Appendix 2.1, Table 2.1). In the upper montane forest, month and air temperature were the significant drivers of soil respiration (p-values = 1.1 x 10^{-9} and 2.2 x 10^{-16}, respectively). Overall, there were no significant seasonal effects but a monthly quadratic relationship was tested to be significant (p-value = 1.1 x 10^{-7}) (Appendix 2.1, Table, 2.2).

At the premontane elevation band, soil VWC, month and land use were the significant drivers of soil respiration (p-value = 0.003, 3.8 x 10^{-5}, 4.7 x 10^{-5}). When testing the sites separately, land-use specific differences were observed, with not all the sites affected by the same variables. For example, soil CO_2 fluxes on the mature forest and abandoned banana soils had a significantly negative relationship with soil VWC (p-value = 0.054 and 0.0008, respectively). On the pasture site, air temperature and month were the main significant drivers of soil respiration (p-value = 0.007 and 0.0001), with decreases in soil CO_2 fluxes observed during months when high air temperatures were measured. Soil respiration on the secondary forest site was positively related to soil temperature, whereas the selectively logged site had a very slight negative relationship with air temperature and there were no significant relationships observed on cultivated banana site (Appendix 2.1, Table, 2.3). March was a particularly dry month, with a sharp decrease in soil VWC on all the sites, which could have biased any seasonal relationships. However, even when this month was excluded from statistical analysis, there were no significant relationships between soil CO_2 flux and season for any of the sites.

3.4.3 Decomposition among the different lands uses and elevations gradients

In montane grasslands, grazing alone appeared to slightly increase the rate of decomposition when all the data were pooled together (grazed: y = 104.53 + -4.23x, R^2 = 0.98, non grazed: y = 103.63 + -3.11, R^2 0.94), but burning alone did not affect decomposition rate (burnt: y = 103.34 + -3.57, R^2 = 0.96, non

burnt: y = 104.82 + -3.76x, R^2 = 0.97). Site-specific differences were observed for decomposition rates, for example, decomposition was generally faster at Wayqecha compared to Acjanaco. Land use also had an effect on decomposition rates. In particular, the grazed - non burnt plot at Wayqecha showed the fastest overall rate of decomposition (y = 101.98 + -0.19x, R^2 = 0.77) and the non grazed - non burnt plots (controls) had the slowest decomposition rates (Figure 3.6) on both sites.

Decomposition was not a strong overall predictor for CO_2 fluxes in montane grasslands, although there were some strong correlations between these two variables at specific study sites. For example, there was a strong relationship between decomposition and soil CO_2 fluxes at Acjanaco (y = 0.38 + -0.18x, R^2 = 0.99) (i.e. faster mass loss = higher soil respiration), whereas at Wayqecha, this relationship was weak (y = 1.56 + 0.06x, R^2 = 0.07). Land-use did not appear to influence the decomposition rate-soil CO_2 flux relationship. Although, this was inconclusive and more data would be required to fully explore this relationship (Appendix 2.1, Table, 2.4).

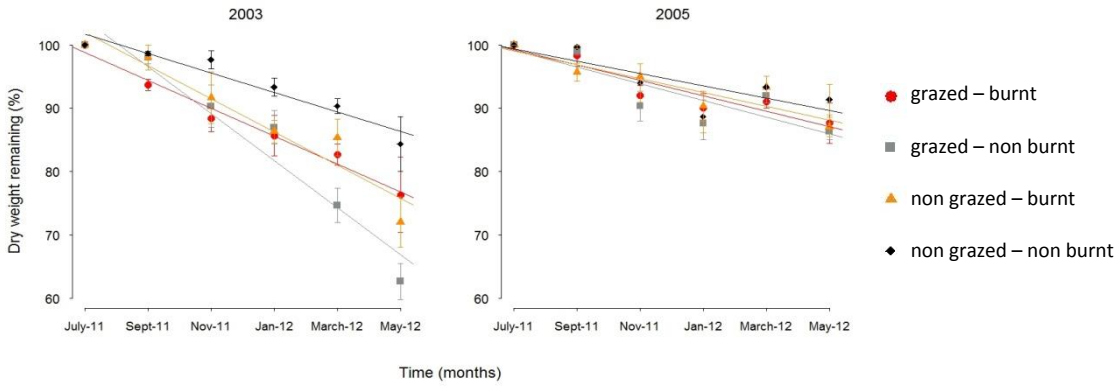


Figure 3.6 Mass losses (%) of sticks from the decomposition experiment on two burnt sites (2003 = Wayqecha and 2005 = Acjanaco) with grazed subplots and control plots for montane grassland (Appendix 2.1, Table 2.5 for regression slopes).

In the montane cloud forest, burning did not appear to alter decomposition rates, but there was a difference among individual study sites. For example, decomposition rates on the burnt Sunchubamba site (2010) were faster than the other sites (Figure 3.7). There was no relationship between decomposition rate and soil CO_2 fluxes among cloud forest sites (y = 0.04x + 1.67, R^2 = 0.01).

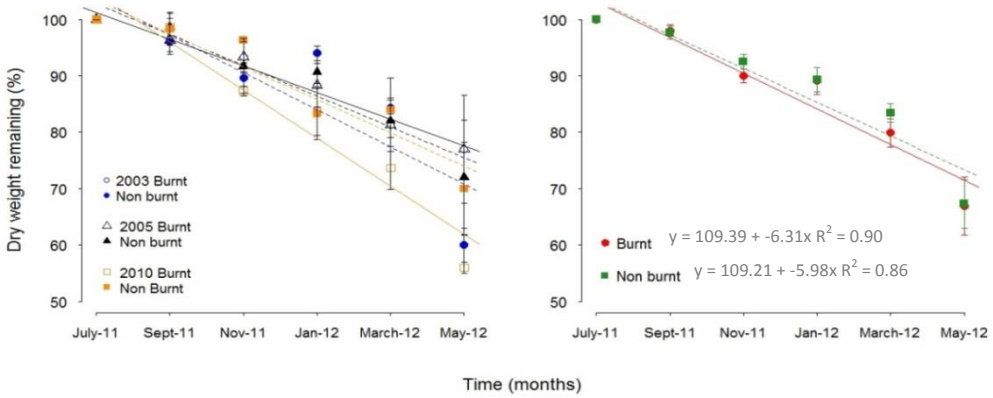


Figure 3.7 Mass losses (%) of sticks against time (months) from the decomposition experiment on three burnt sites (2003, 2005 and 2010) with adjacent non-burnt plots (controls) illustrated on the left graph and on the right the means of all three burnt sites and non-burnt sites in the montane forest. 1 standard error of the means are plotted as error bars (n = 3) (Appendix 2.1, Table 2.6 for regression slopes).

In the premontane forest, decomposition rates were faster on anthropogenically affected sites. For example, the slowest rates were observed on the mature forest (control plot) (y = 132.63 + -17.28x, R^2 = 0.93) and selectively logged forest sites (y = 104.38 + -10.17x, R^2 = 0.38) and fastest on the pasture site (y = 142.36 + -37.01x, R^2 = 0.86) (Figure 3.8). The relationship between decomposition and soil CO_2 flux at this elevation was very strong (y = 0.780 + -0.127x, R^2 = 0.66) i.e. faster mass loss = higher soil respiration).

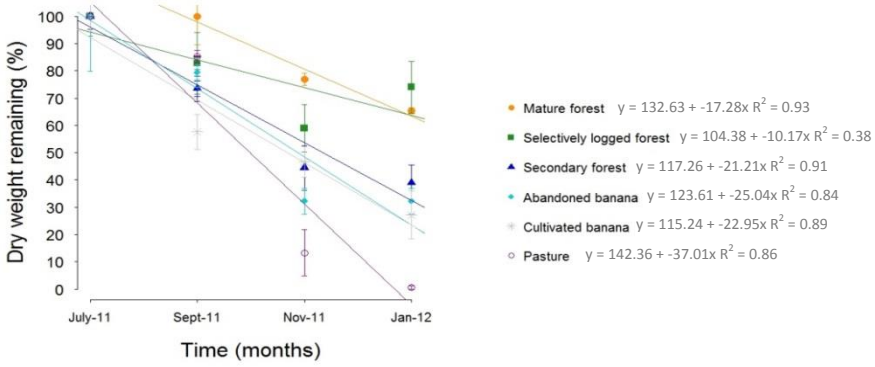


Figure 3.8 Mass losses (%) of sticks from the decomposition experiment on all six land use sites in the premontane elevation.

3.5 Discussion

3.5.1 Soil respiration

Burning and grazing increase soil CO_2 emissions in montane grasslands

Burning and grazing in montane grasslands enhanced soil respiration fluxes and decomposition rates. These land management practices acted on soil respiration by altering local microclimate; in particular, by enhancing air and soil temperatures, thereby promoting higher overall rates of soil respiration. Loss of canopy cover and aboveground biomass probably caused an increase in surface irradiance and energy absorption (Bremer et al., 1998), leading to 1-2 °C rise in temperatures in the managed relative to the control plots. In addition to the independent effect of temperature on respiration itself (Lloyd and Taylor, 1994), temperature also enhanced decomposition rates, and this rise in heterotrophic microbial activity likely contributed to the increase in overall CO_2 efflux. This increase in respiration and decomposition rates may have had a knock-on effect on soil C stocks; although there was not a significant difference in the bulk soil C content, there was a significant reduction in the easily degradable free light fraction (i.e. the soil C pool most vulnerable to decomposition) in the burnt and grazed plots (Chapter 2, Table 2.2 & Figure 2.3). Temperature-driven soil CO_2 fluxes have been observed in high alpine grazing studies before (Cao et al., 2004; Wang and Fang, 2009) but increased rates after burning have also been attributed to the release of dissolved organic carbon and higher NH_4^+ -N concentrations stimulating microbial growth (Andersson et al., 2004).

An exception to the temperature-driven soil CO_2 flux response was on the grazed and burnt plots, which, despite having the highest overall soil respiration rates, had little or no relationship with temperature. The combination of burning and grazing has been known to increase soil respiration rates in other studies (Ward et al., 2007) but the drivers of this increase are less well understood, and the influence of grazing and burning have been known to have conflicting effects (Michelsen et al., 2004). One potential explanation is a synergistic effect of combining burning and grazing, which might obscure the influence of temperature by some other process or driver; such as changes in plant C allocation. For example, studies have found that when foliage is cut, the translocation of C is allocated to the growth of new shoots rather than to the roots (Schmitt et al., 2013), causing a decline in root respiration (García-Oliva et al., 1999). However, the resulting root death enhances microbial activity, counteracting reduced root

respiration. Moreover, infrequent burning can cause significant losses of N from combustion and grasses may compensate for increased N limitation by increasing their allocation to roots, thereby improving root tissue and promoting faster belowground C cycling (Johnson and Matchett, 2001).

In this study, soil CO_2 fluxes from the high elevation montane grasslands ranged from 0.27 to 0.78 Kg C m^{-2} yr^{-1}, which is in the lower range (0.2 – 14.8 Kg C m^{-2} yr^{-1}) of other high elevation montane grassland studies (Geng et al., 2012; Muñoz et al., 2013; Cao et al., 2004; Fu et al., 2014) but does corroborate with a previous study on the same sites (Oliveras et al., 2014). The absence of a seasonal trend in temperature and moisture has also been noted in other studies from the same region (Teh et al., 2014; Girardin et al., 2013). Overall, the plots at Wayqecha (burnt in 2003) had consistently higher soil respiration rates than at Acjanaco (burnt in 2005). However, this may not be a reflection of the age of burning but rather Acjanaco being at a slightly higher elevation than Wayqecha and on average 4 °C cooler. Despite the variance in mean annual temperature, the two sites both showed a positive correlation between temperature and soil respiration, which further supports the importance of temperature in this ecosystem.

No medium to long-term impacts of burning on soil CO_2 emissions in upper montane forest

The effect of burning and time since burning did not significantly affect mean annual soil respiration or decomposition rates in the medium to long-term (i.e. on multi-annual timescales). However, the loss of total C content in the surface soils, which ranged from 14 – 50 % (Chapter 2, Table 2.4), is consistent with previous upper montane forest studies, which report that up to 90 % of the original soil C can be lost after burning (Román-Cuesta et al., 2011; Asbjornsen et al., 2005). This suggests that the loss of soil C may not be due to long-term changes in decomposition rates, but rather the direct effect of smouldering fires in these highly organic-rich peaty soils (Delaney et al., 1997). There may be several reasons why no net change in soil respiration was observed in upper montane forest. One explanation is that recovery of the large root biomass (4.95 Mg C ha^{-1}) (Girardin et al., 2013) and the litter layer over several years may have offset any short-term (<1 year) changes in heterotrophic respiration arising from loss of the forest floor and O horizon. Another possibility is that enhanced soil temperatures (see table 3.3) in burnt areas, due to microclimate changes following burning, may have led to an overall shift towards higher soil respiration rates, offsetting any changes in respiration due to a reduction in organic matter stocks in the

forest floor and O horizon. Lastly, if the majority of the soil respiration in these soils arises from the organic-rich mineral horizons (60.4 ± 11.6 Mg C ha-1 at 10-20 cm, Chapter 2, Table 2.4), then fire damage to the forest floor and O horizon, which contain a much smaller proportion of overall C stocks in this system (5.3 ± 0.7 Mg C ha-1 at 0-10 cm, Chapter 2, Table 2.4), may have made little impact on net soil CO_2 efflux (van Reenen et al., 1992).

Although burning did not significantly affect soil respiration rates in the medium to long-term, the decomposition rates on the most recently burnt site (2010) were faster than the unburnt sites, and an initial spike in soil respiration was measured the day after the fire occurred in July 2011. This was to be expected, as increases in CO_2 fluxes usually occur for a few days after burning because of the release of nutrients from the humus and incompletely burnt OM stimulating microbial activity (Asbjornsen et al., 2005). Even if some of the microbes are killed during fire, soil respiration can increase because of the surge in dead cells and decomposing roots. The increase in pH on the burnt plot (Table 3.3), which occurs from the release of alkaline ions after fire (Nye and Greenland, 1964), should have in theory, favoured decomposition rates in these normally acidic, nutrient poor soils (Vitousek, 1984; Certini, 2005) and the faster decomposition rates would suggest this was the case. However, two months after burning, the soil CO_2 fluxes decreased by 60 % and continued at lower levels than the control plot for the rest of the year. This can be explained by the immediate loss of vegetation, litter, and surface SOM (Luo and Zhou, 2010). Furthermore, these forests sit on very steep sided slopes (~ 28 %) (Girardin et al., 2013) and leaching may be exacerbated during the rainy season with the loss of vegetation and organic matter (Gonzalez-Perez et al., 2004; Osman, 2012; Brady and Weil, 1996).

Time of year and air temperature were the main drivers of soil respiration in the upper montane forests with an increase during the wetter months. This is in keeping with seasonal patterns observed in other cloud forest studies (Girardin et al., 2010; Zimmermann et al., 2009b; Sotta et al., 2007), and is explained by an increase in heterotrophic respiration from the breakdown of accumulated litter fall from the dry season (Metcalfe et al., 2007).

Pasture conversion in the premontane tropics enhances soil CO_2 emissions

Pasture soils had significantly higher soil CO_2 fluxes and faster decomposition rates compared to all the other agricultural and forest sites. Soil CO_2 fluxes in pasture were primarily driven by temperature; a common finding among tropical grassland studies (Salimon et al., 2004) because of their fast C turnover rates and greater allocation to belowground C. Total soil C was significantly smaller in the pasture soils and generally had a smaller proportion of labile free light fraction than the forest soils (Chapter 2, Table 2.5), which suggests a rise in heterotrophic activity due to the warmer temperatures. The mature forest had very similar soil respiration rates to the agricultural and secondary forest soils, but the decomposition rates and other environmental drivers of respiration differed; a finding that has also been reported in Malaysian tropical studies (Melling et al., 2014; Adachi et al., 2006; Salimon et al., 2004). Notably, the mature forest had the slowest decomposition rates, and soil CO_2 fluxes were significantly related to soil VWC content, along with the abandoned banana soils. This is in contrast to other land-uses, where soil CO_2 fluxes were more strongly linked to soil and air temperature.

It is not surprising that soil VWC was negatively correlated with soil respiration for the mature forest and abandoned banana as it is well established that soil moisture content influences soil respiration in tropical soils (Davidson et al., 2000a) and has been identified for explaining temporal and spatial variations in other tropical studies because of the large fluctuations in precipitation in tropical ecosystems (Schwendenmann et al., 2007; Salimon et al., 2004; Hashimoto et al., 2004). However, all the sites had similar VWC (~46 %) and so the lack of a moisture response on the other land uses was unexpected. A potential reason may be due to texture affecting soil porosity (Thomsen et al., 1999; Franzluebbers, 1999; Bouma and Bryla, 2000). The abandoned banana and mature forest soils were sandy and therefore may have had lower holding capacities relative to the silty soils found on the other land uses (Silver et al., 2000).

Soil respiration rates from the mature forest were similar to other tropical studies (Raich, 1998; Raich and Schlesinger, 1992; Fernandes et al., 2002) but in general were slightly lower (1.05 ± 0.11 Kg C m^{-2} yr^{-1}) than reported values (0.5 – 2.3 Kg C m^{-2} yr^{-1}) (Schwendenmann et al., 2003; Zimmermann et al., 2010b;

Doff Sotta et al., 2004; Trumbore et al., 1995; Metcalfe et al., 2007). However, most of these studies were at elevations lower than 500 m a.s.l in tropical lowland forests where warm temperatures prevail.

3.6 Conclusions

The impact of land use change on soil C stocks and respiration has been gaining momentum in scientific research and it is particularly pertinent to the vast but fragile tropical environment in the Andes, with its high C density and vulnerability to changes in land cover and land management. The results of our site investigations have shown that such impact is considerably in certain situations and less so in others. In cases where soil respiration appears to be affected by land-use, the most plausible explanation is that the mechanism or reason for this change is an altered microclimate, particularly an enhanced surface/soil temperature with accelerated microbial decomposition rates. In such cases of greater decomposition and soil respiration there appears to be evidence of a 'knock-on' effect on soil C stocks.

Most specifically, our study shows that land management affected the magnitude and drivers of soil respiration and decomposition rates in the montane grasslands and premontane forest, but not the upper montane forest. In the montane grasslands, burning and grazing increased soil CO_2 fluxes and the overall driver was temperature. However, the combined effect of burning and grazing caused a synergistic effect which obscured the influence of temperature, potentially a result of C and N allocations. In the upper montane forest, burning did not affect soil respiration rates and variances in fluxes were explained by time of year and air temperature, but there were only significant losses in total C at one of the sites. At the premontane elevations, pasture was the only land use to have a significant effect on soil respiration, but the environmental drivers affecting flues were altered and surprisingly, the most influential driver on the agricultural land uses was temperature, rather than the well-established soil moisture content that affects tropical forest soils.

This study highlights the complexities of how land management can affect soil respiration in different ecosystems and points to the limitations in existing research and understanding of the human impact on enhanced soil CO_2 fluxes in tropical montane ecosystems. Extensive focussed research is needed on a larger number of replicates of the same type of land use and should include soil microbiology, nutrient and belowground biomass. Furthermore, an intensive short term study is needed on how land use might affect soil CO_2 fluxes with an altered soil moisture content/ precipitation, and how these gases might respond to future climate changes.

~ Chapter 4 ~

Sensitivity of soil respiration to land-use and the combined influence of soil temperature and moisture in agricultural soils from the tropics

Tropical montane cloud forest in Andean Peru. Photograph by Viktoria Oliver.

4.1 Abstract

Tropical soils are one of the largest contributors to global soil respiration and account for one third of the world's soil carbon (C). The main controls of soil respiration are temperature, moisture and substrate quality and quantity but despite their synergistic relationship, tropical soil C cycling research has generally explored these factors separately. With the predictions of climate changes and further deforestation and land-use change in the topics, it is important we gain a better understanding of how these factors interact for future modelling of climate change scenarios. This study has focused on the interactions of these important drivers of soil heterotrophic respiration on four different land-uses from the Peruvian tropical forest using a short-term incubation experiment on intact soil cores. Four temperatures were used (16 °C, 24 °C, 28 °C, 32 °C) and three moisture treatments (25-45 %, 45-65 % and 65-85 % volumetric water content (VWC)). Temperature increases generally caused an exponential rise in soil respiration in all the sites and the response of heterotrophic respiration to soil moisture varied according to study site. For mature forest soils, respiration was inversely proportional to moisture, with a more pronounced relationship observed at higher temperatures. For abandoned banana plantations, respiration and moisture were positively correlated except at the highest temperature (32 °C), when the two variables had the opposite effect. Soil moisture caused a slight increase in CO_2 flux on the cultivated banana soils, except at the lowest temperature (16 °C). Pasture soils were not significantly affected by soil moisture, although there was a trend of a decreasing CO_2 flux at the highest moisture treatment (65-85 %). This study confirms expected trends in tropical soils: higher soil temperatures result in an exponential increase in CO_2 emissions. However, contrary to theoretical expectations, soil moisture was not the dominant driver of heterotrophic soil respiration, unless at higher temperatures where soil moisture then became the dominant factor. Furthermore, the land-use history of soil is critical in determining how emissions of CO_2 respond to soil moisture and temperature. These factors must be considered when predicting the effects of climate change in regions expected to change in both temperature and precipitation.

4.2 Introduction

Recent research has shown that the controls and magnitude of long-term soil CO_2 fluxes are key uncertainties in the global carbon (C) cycle (Davidson and Janssens, 2006; Reichstein et al., 2005a). Temperature, moisture, substrate quality and quantity are the main controlling factors in the biochemical breakdown of soil organic matter (SOM) and the subsequent release of CO_2 to the atmosphere (Kutsch and Heinemeyer, 2010; Bosatta and Ågren, 1999; Fierer et al., 2005; Trumbore et al., 2006; Schimel et al., 1994; Ise and Moorcroft, 2006). Changes to these environmental controls, as a result of changing land-use or climate, may alter edaphic processes and either increase or decrease SOM decomposition rates (Raich and Schlesinger, 1992; Reiners et al., 1994; Davidson et al., 2000a; Hagedorn et al., 2010). The complex interactions among these processes and controls mean that the rate limiting factors can differ with environmental conditions; this has challenged soil C cycling research, often leading to contrary results being reported (Craine and Gelderman, 2011; Suseela et al., 2012).

The temperature sensitivity of SOM decomposition on tropical soils has been highlighted in both laboratory and field soil warming experiments and is generally expressed as an exponential curve with larger CO_2 fluxes from soils at higher temperatures (Balser and Wixon, 2009; Holland et al., 2000; Wood et al., 2012; Bekku et al., 2003), suggesting that in a warmer world, SOM decomposition would be greater. This supports the kinetic theory that reaction rates increase with elevated temperature (Davidson and Janssens, 2006) and can be explained by the acceleration in extracellular enzyme activity that degrades polymeric SOM (Wallenstein et al., 2011). The temperature response of tropical soils, represented using the Q_{10} function, has been reported to be 2.1 at 24 °C, which increases with cooling down to 16 °C but does not change with warming up to 32 °C (Bekku et al., 2003).

In tropical ecosystems, soil C fluxes are thought to be dominated by precipitation and water availability (Werner et al., 2006; Butterbach-Bahl et al., 2004; Vasconcelos et al., 2004). Theory suggests that extremes of low and high soil moisture can significantly affect soil respiration rates and the coupling with the atmosphere, producing a peak in respiration at moderate soil moistures. For example, high soil moisture can suppress microbial and root respiration by limiting oxygen, which indirectly affects substrate supply and the release of CO_2 (Linn and Doran, 1984; Davidson et al., 2006; Sjögersten and

Wookey, 2002; Skopp et al., 1990), whereas, during periods of low soil moisture, respiration can be suppressed because decomposition of SOM relies on soluble C substrates and enzymes diffusing in the aqueous phase of the soil (Grant and Rochette, 1994). However, despite this knowledge, soil moisture manipulation studies have disparate findings when it comes to the magnitude and direction of the soil respiration response with altered soil moisture availability (Davidson et al., 2004; Metcalfe et al., 2007; Sotta et al., 2007; Wieder et al., 2009). For example, (Wood and Silver, 2012) found that humid tropical forests in Puerto Rico have the potential to decrease soil respiration during periods of droughts. Likewise, an induced drought using a throughfall exclusion experiment in an eastern Amazonian rainforest in Brazil reported a decrease in soil CO_2 production (Sotta et al., 2007), whereas in the tropical rainforest in Costa Rica, (Cleveland et al., 2010) found an increase in CO_2 efflux with drought. This may be a reflection of the heterogeneous nature of tropical soils, complexity of environmental drivers, regional differences in climate and experimental designs across these studies.

Soil temperature and soil moisture are known to influence soil respiration in most ecosystems, however, information on the combined effects of both factors on soil respiration is scarce (Bowden et al., 1998; Curiel Yuste et al., 2007; Davidson et al., 2006). One recent field study which took place in the humid tropical forests in Puerto Rico found that the positive effect on soil respiration normally seen with increasing temperature was constrained by soil moisture availability (Wood et al., 2013). However, studies of the potentially synergistic interactions among temperature, moisture and respiration in tropical soils are rare, even though this information is essential for explaining and modelling the process-level behaviour of heterotrophic communities. Even less is known about whether these temperature, moisture and respiration relationships are affected by land-use change (Craine and Gelderman, 2011), particularly in the tropics.

Understanding the relationship among temperature, moisture and respiration is critical within the context of tropical deforestation and land-use change, because enhanced respiratory losses of C after forest clearing are a major source of atmospheric CO_2 (Malhi, 2010). Moreover, clearing vegetation often precipitates major shifts in microclimate and hydrology, which may alter temperature and moisture conditions in disturbed habitats. Changes in vegetation affect SOM decomposition by altering the litter

quality, belowground C allocation and soil microbial communities (Zogg et al., 1997; Moyano et al., 2012; Reichstein et al., 2005b), which may then result in different temperature sensitivities. There may also be changes in the proportions of labile and recalcitrant C pools, which may have different temperature sensitivities (von Lützow and Kögel-Knabner, 2009). In addition, surface soil temperature and moisture are altered after land-cover change due to a reduction in canopy cover (albedo effect and partitioning of latent and sensible heat) and changes to the physical characteristics of the soil, such as: porosity and organic matter content (Gabriel and Kellman, 2011). Concurrent changes in climate and rapid rates of land-cover changes that are occurring in the tropics will undoubtedly cause changes in the abiotic and biotic controls on respiration (Sala et al., 2000; McCulley et al., 2007).

Most tropical soil respiration studies have concentrated on field based observations or in-situ warming experiments with a minority focusing on soil moisture manipulation (Vicca et al., 2014). While field based studies are critical for understanding ecosystem C budgets and the response of net respiration fluxes to environmental drivers, it can be difficult to investigate the finer scale controls of soil respiration using only field-based data because gross respiration may be confounded by other factors (Davidson and Janssens, 2006) and the difficulty of separating autotrophic and heterotrophic respiration (Ryan and Law, 2005). Incubation experiments, where moisture and temperature are controlled, are particularly useful as they allow for the investigation of the interactive and synergistic effects of varying water and temperature on heterotrophic respiration. Although there are some drawbacks to incubation experiments, incubating soils for a shorter period of time is the least biased way to estimate temperature sensitivities of SOM decomposition and can be more representative of field conditions, rather than providing information on the overall size of the soil organic carbon (SOC) pools of different recalcitrance, which often occurs during long-term incubation (Dalias et al., 2001; Chen et al., 2010). Short-term incubation experiments are not confounded by a decline in substrate availability (Wetterstedt et al., 2010) or thermal adaptation of microbial communities (Balser and Wixon, 2009) and isoenzymes (Bradford et al., 2010).

This study aims to determine the combined influence of soil moisture and temperature on heterotrophic respiration from soils with different land-use histories. A short term incubation study using a factorial experimental design (with soil temperature ranging from 16 to 32 ^{o}C RW- seems a large range and soil

moistures from 25 to 85 %) was carried out on soils under four different land-uses from the Peruvian montane tropical forests (undisturbed forest, active banana cultivation, abandoned banana cultivation and pasture). The motive for choosing these sites was based on a one year observational field experiment conducted in 2012, which raised questions as to why certain land-uses had different soil moisture and temperature relationships with soil respiration and so we wanted to further explore these interactions in a controlled laboratory setting (chapter three for more details of the field study and the chosen sites).

Key research objectives were:

1. To determine the response of heterotrophic respiration from soils with different land-uses to systematic variations in soil temperature;
2. To determine the response of heterotrophic respiration from soils with different land-uses to systematic variations in soil moisture;
3. To establish whether altered soil moisture content would modify the temperature sensitivity of heterotrophic respiration among soils from differing land-uses.

4.3 Methods

4.3.1 Site description

The study area is located at Villa Carmen Biological Reserve, which is a 3070 ha abandoned farm recently purchased by La Asociación para la Conservación de la Cuenca Amazónica (ACCA), situated at the confluence of the Rio Pini Pini and Rio Tono rivers. The mean annual temperature is 22 °C with 4500 mm mean annual precipitation. The natural vegetation at this altitude (520-1200 m a.s.l) is premontane rainforest. Soils are typically acidic, sandy loams with an average bulk density of 0.99 g cm^{-3} (Table 4.1). The land-use sites used in this experiment were: mature forest (VC-F), cultivated banana (VC-BC), abandoned banana (VC-AB) and pasture (VC-P).

Table 4.1 Site and soil description for all four sites in Villa Carmen

Site code	**VC-F**	**VC-AB**	**VC-B**	**VC-P**
Site history and vegetation	Undisturbed forest-Premontane rainforest	Abandoned banana-8 years ago	Active banana cultivation	Pasture- cattle grazing
Elevation (m a.s.l)	580	521	527	508
Coordinates	12°53.072'S 071°25.530'W	12°53.293'S 071°23.920'W	12°53.294'S 071°23.920'W	12°53.397'S 071°24.242'W
Texture	60/36/4	46/51/3	24/71/4	62/36/3
pH	5.1 ± 0.2	5.7 ± 0.3	5.6 ± 0.6	5.6 ± 0.1
Bulk density 0-10 cm (g cm^{-3})	0.99 ± 0.01	1.05 ± 0.02	0.92 ± 0.02	1.01 ± 0.01
Bulk C stock 0-30 cm (Mg C ha^{-1})	28.4 ± 2.4	20.4 ± 1.9	16.3 ± 0.5	19.1 ± 1.7
Bulk C 0-5 cm (%)	3.3 ± 1.1	3.1 ± 1.7	1.9 ± 0.5	2.1 ± 0.9
Bulk $\delta^{13}C$ (0-5 cm)	-28.6 ± 0.4	-28.3 ± 0.7	-29.0 ± 0.5	-19.3 ± 1.2
Mean annual soil temperature (°C)	23.2 ± 1.0	23.1 ± 1.8	24.5 ± 2.0	26.5 ± 2.2
Wet season mean annual soil temp. (°C)	23.7 ± 0.9	24.2 ± 0.9	25.5 ± 1.1	28.2 ± 1.8
Dry season mean annual soil temp. (°C)	22.6 ± 0.8	22.2 ± 1.4	23.5 ± 2.1	25.1 ± 1.4
Minimum measured soil temp. (°C)	22.4	18.7	18.3	20.8
Maximum measured soil temp. (°C)	31.4	26.1	28.6	27.2
Mean annual soil VWC (%)	46.1 ± 5.6	45.6 ± 5.1	50.1 ± 3.7	47.2 ± 5.3
Wet season mean annual soil VWC (%)	46.8 ± 5.7	44.6 ± 5.1	49.7 ± 3.9	45.9 ± 6.0
Dry season mean annual soil VWC (%)	45.3 ± 5.5	46.4 ± 5.3	50.5 ± 3.5	48.4 ± 4.4
Minimum measured soil VWC (%)	32.4	32.21	36.4	26.0
Maximum measured soil VWC (%)	56.3	56.42	57.8	57.9
Mean annual soil CO_2 flux (µmol/m^2/s)	2.76 ± 2.09	3.54 ± 1.58	3.00 ± 1.52	6.18 ± 3.44

Bulk densities and C stocks (0-10 cm) are given with 1 standard error of the mean (n = 3 and n = 6, respectively) and values for texture represent proportions (%) of sand/silt/clay (n = 3). Mean soil temperature and volumetric water content (VWC) are at 0-10 cm depth from in-situ measurements (n = 18) taken every two months between July 2011 and July 2012.

4.3.2 Soil sampling

During the wet season, on 20th January 2014, twenty one intact soil cores were collected from each land-use site by inserting polyvinyl chloride (PVC) pipes (75 mm inner diameter and 100 mm deep) at randomly chosen locations in a 30 x 30 m^2 area. The soil cores were securely sealed and immediately shipped from Peru to the University of Stirling. VWC was measured by taking subsamples from every core, which were then weighed before and after drying at 105 °C for 24 hours. Using the measured VWC of each soil core and its initial weight, the amount of additional deionized water was calculated to make up the three moisture treatments or in some cases, dried to obtain 25% VWC. If there was any vegetation growing within the cores, this was cut prior to incubation. In order to recover from any sampling and transport disturbance the soil cores were then left to equilibrate to laboratory conditions (25 °C) for seven days before soil respiration measurements started. Soil bulk C, bulk density, soil texture, pH and isotope data were collected during the long term observational study; methods are described in chapter three and results are summarised in Table 4.1.

4.3.3 Experimental design

This laboratory study followed a 2-factor block design, with temperature and moisture as independent variables and soil CO_2 efflux as the dependent variable. Four temperature treatments (16 °C, 24 °C, 28 °C, and 32 °C) and three soil moisture treatments (20-40 %, 40-60 % and 60-80 % VWC) were used. The temperature and moisture treatments were selected to detect maximal effect of both cooling and warming, based on data collected from an *in situ* experiment previously conducted on the same sites (Appendix 3.1 in Figures 3.1, 3.2, Table 3.1 and Chapter 3, Table 3.4 & Figure 3.4). In the field experiment, moisture was normally distributed for all the sites with the highest frequency of volumetric water content in the range of 50 and 60 %. Temperature was normally distributed for V-F, V-B and V-AB with the highest frequency of temperatures ranging between 23 °C and 25 °C. Pasture had a bi-model distribution with average morning temperatures of 25 °C and afternoon soil temperatures of 28 °C. Significant relationships were found between volumetric water content and CO_2 on V-F and V-AB and a significant relationship between temperature and CO_2 for V-P. The reason for choosing 16 °C was to test the lower

limits of what would normally be found at field temperature and is in keeping with another study looking at soil warming and cooling in tropical soils (Bekku et al., 2003).

To avoid the potentially confounding treatment effects, where CO_2 flux may decline over time since the start of the experiment (Chen et al., 2010) due to disturbance effects or depletion of labile organic matter, the replicates were split and incubated in blocks of six at the four different temperatures simultaneously. Four incubators (MIR-153, SANYO, Loughborough, UK) were concurrently used during the experiment to avoid the confounding effects of a time trend, where CO_2 flux declines over time due to a lack of vegetation inputs, irrespective of temperature or soil moisture content. Twenty one soil cores were placed in all four incubators and each incubator set to one of the four temperatures treatments (16 °C, 24 °C, 28 °C and 32 °C). After five days, the temperatures were either increased or decreased and this process was repeated every five days until the four incubators had been set to all the temperatures treatments over the course of twenty days. This allowed every soil core to be measured at each of the four temperatures but run through the sequence of temperature treatments in a different order (Table 4.2). The moisture treatments were represented equally within every incubator with seven soils cores of each moisture treatment in one incubator to avoid the potential bias from the time since the start of the incubation. Due to drying, the soil cores were weighed every other day and additional deionized water added if required. Depending on the temperature, approximately 2 - 5 ml was needed to obtain the correct soil core weight. To avoid the associated effects of ebullition (bubble transport), watering was done the night before any measurements took place.

Table 4.2 Experimental set up (AB = Abandoned banana; BC = Cultivated banana; F = Mature forest; P = Pasture)

Temperature sequence	**VWC (20-40 %)**				**VWC (40-60 %)**				**VWC (60-70 %)**			
Incubator 1:	F-1	AB-1	B-1	P-1	F-3	AB-3	BC-3	P-2	F-4	AB-5	B-5	P-4
16 °C – 24 °C – 28 °C – 32 °C	F-2	AB-2	B-2			AB-4	BC-4	P-3	F-5		B-6	P-5
Incubator 2:	F-6	AB-6	B-7	P-6	F-8	AB-7	BC-9	P-8	F-10	AB-9	B-10	P-10
24 °C – 28 °C – 32 °C – 16 °C	F-7		B-8	P-7	F-9	AB-8		P-9		AB-10	B-11	P-11
Incubator 3:	F-11	AB-11	B-12	P-12	F-12	AB-13	BC-14	P-14	F-14	AB-15	B-16	P15
28 °C – 32 °C - 16 °C – 24 °C		AB-12	B-13	P-13	F-13	AB-14	BC-15		F-15	AB-16		P-16
Incubator 4:	F-16	AB-17	B-17	P-17	F-18	AB-19	BC-18	P-19	F-20	AB-20	B-20	P-21
32 °C – 16 °C – 24 °C – 28 °C	F-17	AB-18		P-18	F-19		BC-19	P-20	F-21	AB-21	B-21	

4.3.4 Gas measurements

During the twenty day period of incubation, the vents were left open to avoid a build-up of CO_2 in the closed incubator environment. Respiration measurements were carried out every 5 days using an infra-red gas analyser (EGM-4, PP Systems, Hitchen, UK) connected to a 700 ml Lock & Lock ® container in a closed loop configuration. Soil cores were temporarily taken out of the incubators and placed inside the sealed container and the rate of CO_2 accumulation was measured every 0.5 seconds for 3 minutes, along with air temperature measurements within the chamber. The headspace concentration (ppm) was plotted against time (minutes) for each core using the R package 3.0.2 (R Core Team, 2012) and HMR to determine the flux rates (Pedersen et al., 2010). The Ideal Gas Law was then used to convert gas mixing ratios to areal fluxes to solve for quantity of CO_2 in the headspace in moles (Livingston and Hutchinson, 1995) using the following equation:

$$n = PV/RT \quad \text{[Eq. 1]}$$

where n is the number of moles of CO_2 gas (mol), P is atmospheric pressure (assumed to be 1 atm), V is the volume (L), R is the idea gas constant (0.08205 L atm $°K^{-1}$ mol^{-1}), and T is temperature (K) (Livingston and Hutchinson, 1995). Fluxes were then reported in µmol m^{-2} s^{-2}.

4.3.5 Temperature sensitivity calculations

Temperature sensitivity of soil respiration was expressed as the van't Hoff's temperature coefficient Q_{10} and determined using Eq. 1:

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{10(/T_2 - T_1)} \quad \text{[Eq. 1]}$$

where Q_{10} is the factor by which the reaction rate (R) increases for every 10 °C rise in temperature (T). CO_2 was used as the proxy for the reaction rate. R_1 is the measured reaction rate at temperature T_1 and R_2 is the measured reaction rate at temperature T_2. Although the Q_{10} is a convenient way to examine and report the temperature dependence of soil respiration between two temperatures, the Arrhenius equation

(Eq. 2) was also used to describes changes in the respiration rates over the four temperatures used in this study. This model predicts that as temperature increases, the respiration activity approaches some constant value,

$$k = A \exp(-Ea/(RT)) \quad \text{[Eq. 2]}$$

where k is the reaction rate constant; A is the frequency factor; E_a is the required activation energy in joules per mole; R = 8.314 J K^{-1} mol^{-1} gas constant and T is the temperature, which is expressed in Kelvin in the model. The activation energy (E_a) was calculated using the slope of the regression line when the natural logarithm of CO_2 fluxes was plotted with the inverse of temperature (ln K vs (1/T)).

4.3.6 Statistical analyses

Statistical analyses were performed using the R package 3.0.2 (R Core Team, 2012) and *lme4* (Bates et al., 2014) to perform mixed model restricted maximum likelihood analysis (REML) with repeated measures, which identified any main relationships between soil moisture and temperature with soil CO_2 flux among the four sites. The linear mixed model takes into account the violation of independence from repeating measurements on the same cores and also the nested design of the experiment, which included three moisture treatments for each temperature treatment. Site, VWC and time were entered as fixed effects in the model and temperature as random effect, as well as by-core random slopes for the effect of soil CO_2 flux. Prior to analysis, no outliers were detected and data were checked for normal distributions using histograms, QQ plots and the Shapiro-Wilk test. The CO_2 flux data had a skewed distribution and was therefore log transformed prior to parametric statistical analysis. Model selection and significance (reported at $p < 0.05$) was obtained by using likelihood ratios and Akaike information criterion (AIC) of the full model with the effect in question against the model without the effect in question. Residuals were visually assessed for large deviations from assumptions of homogeneity and normality (Zuur et al., 2009). Analysis of variance (ANOVA) and Tukey's Honest Significant Different (HSD) post hoc test were used to examine statistically significant differences between means among treatments and sites. Linear regression analysis was used to examine the individual relationship of soil moisture and temperature with CO_2 flux for each site.

4.4 Results

4.4.1 Temperature sensitivity of soil respiration

Irrespective of the soil moisture content, temperature alone had a very significant effect in increasing soil respiration rates on all the soils from the four sites, with similar linear regression slopes. The standard error of the slope for the abandoned banana was 0.005 with and 38 % of the variance explained by temperature. The cultivated banana had the highest R^2, showing that 60 % of variance in the data was explained by temperature with a standard error of 0.003. The mature forest and pasture soils had similar R^2 values with 52 and 50 % of variance in the data explained by temperature and small standard errors of the slope (0.004). There were also no obvious signs of decreasing fluxes at higher temperatures (Figure 4.1). The highest mean rates of soil respiration were measured on the pasture soils at 32 °C (0.85 ± 0.50 µmol/m^2/s) with the lowest on the cultivated banana soils at 16 °C (0.18 ± 0.09 µmol/m^2/s). However, there were no statistically significantly different fluxes between the sites at any of the four temperatures. The higher temperatures had generally larger standard deviations and outliers in comparison to the lower temperatures (Figure 4.2), although this was less for the abandoned banana soils (Figure 4.3 and Appendix 3.1, Table 3.2 for full details of individual site regressions).

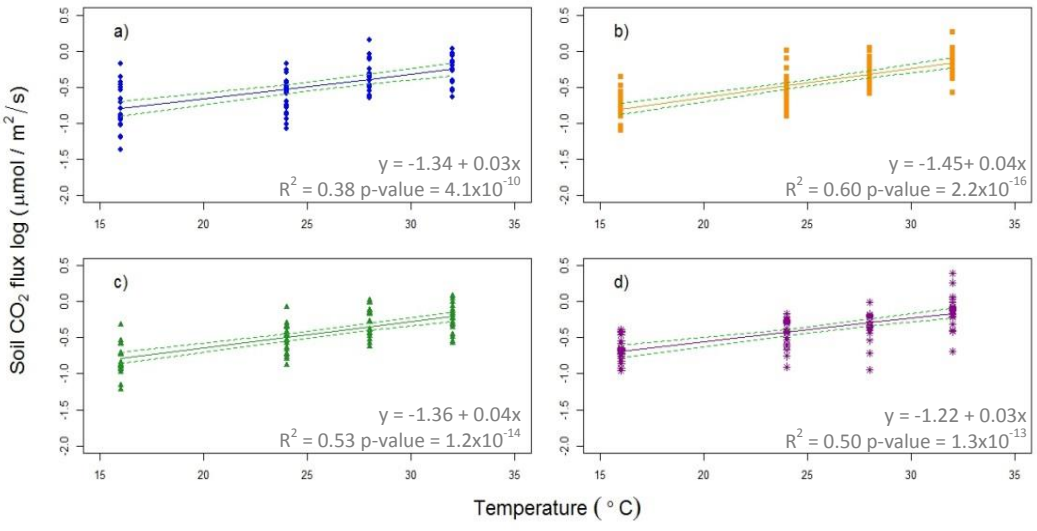


Figure 4.1 Linear relationships between logged soil CO_2 fluxes (µmol / m^2 / s) and temperature on the four different soils (a) abandoned banana; b) cultivated banana; c) mature forest; d) pasture). Green dashed lines represent 95 % confidence limits for the data. Regression details are given in the bottom right corner for each site.

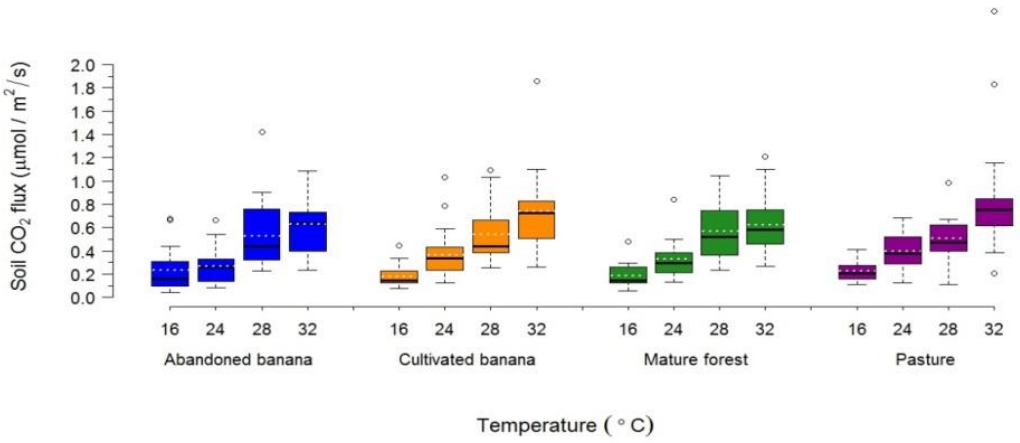


Figure 4.2 Mean CO_2 fluxes (µmol / m^2 / s) from the 24 day incubation experiment (n = 24 per site) under four temperatures (16 °C, 24 °C, 28 °C, 32 °C) with soils (0-10 cm) from four different sites (abandoned banana = blue, cultivated banana = orange, mature forest = green, pasture = purple). Boxes enclose the interquartile range, whiskers show the full range. Dashed white lines represent the means and solid black lines represent the median values.

The $\boldsymbol{Q_{10}}$ values and activation energies for mean and individual moisture treatment of each site are reported in table 3. $\boldsymbol{Q_{10}}$ ranged from 1.16 to 6.12 but the standard deviations were very high for all the values. Mean $\boldsymbol{Q_{10}}$ values (all moisture treatments combined), showed an increase in the mid-range of temperatures (24 : 28 °C) and a decrease at the higher and lower temperatures for all the sites, although, this pattern was less pronounced on the pasture soils. Splitting the $\boldsymbol{Q_{10}}$ into moisture treatments reduced the large standard errors slightly and showed mixed responses between treatments and sites, with the highest $\boldsymbol{Q_{10}}$ still generally positioned at 24:28 °C. The activation energies between the sites were very similar with the cultivated banana showing the highest at 69 KJ mol^{-1}. The mature forest had the highest activation energy with the M2 moisture treatment (45-65 % VWC). The activation energies were calculated using the slopes from the relationship between natural logarithm of the CO_2 flux and 1/temperature.

Table 4.3 Mean Q_{10} values for temperatures between 16 and 24 °C, 24 and 28 °C and 28 and 32 °C on all four sites and the activation energy using the Arrhenius equation for all data and for individual moisture treatments.

Site & treatment	Q_{10}			*Ea* (kJ mol^{-1})
	16 : 24 °C	24 : 28 °C	28 : 32°C	
VC - AB	**1.62 ± 1.12**	**2.65 ± 1.99**	**1.72 ± 1.16**	**57**
M1	1.22 ± 0.54	2.51 ± 2.00	1.61 ± 1.45	63
M2	2.12 ± 1.50	1.86 ± 0.76	1.56 ± 0.87	58
M3	1.46 ± 0.96	6.12 ± 2.96	1.94 ± 1.11	50
VC - BC	**2.75 ± 1.59**	**3.14 ± 1.68**	**1.61 ± 1.15**	**69**
M1	2.93 ± 0.81	4.24 ± 2.63	2.02 ± 1.47	61
M2	3.97 ± 1.26	2.77 ± 1.56	1.43 ± 0.88	71
M3	2.74 ± 1.66	3.04 ± 2.55	1.05 ± 0.79	75
VC - F	**2.60 ± 1.62**	**3.24 ± 2.14**	**2.37 ± 2.22**	**64**
M1	2.85 ± 2.12	2.80 ± 2.06	2.41 ± 2.38	59
M2	3.11 ± 1.16	3.09 ± 1.35	3.10 ± 2.66	82
M3	2.14 ± 1.53	3.96 ± 3.27	1.16 ± 1.04	50
VC - P	**2.53 ± 1.86**	**2.89 ± 2.17**	**2.67 ± 1.56**	**58**
M1	2.48 ± 1.90	3.06 ± 2.81	2.29 ± 1.98	55
M2	2.14 ± 1.14	3.27 ± 2.28	2.76 ± 0.94	57
M3	2.97 ± 2.49	2.27 ± 1.46	3.37 ± 1.98	61

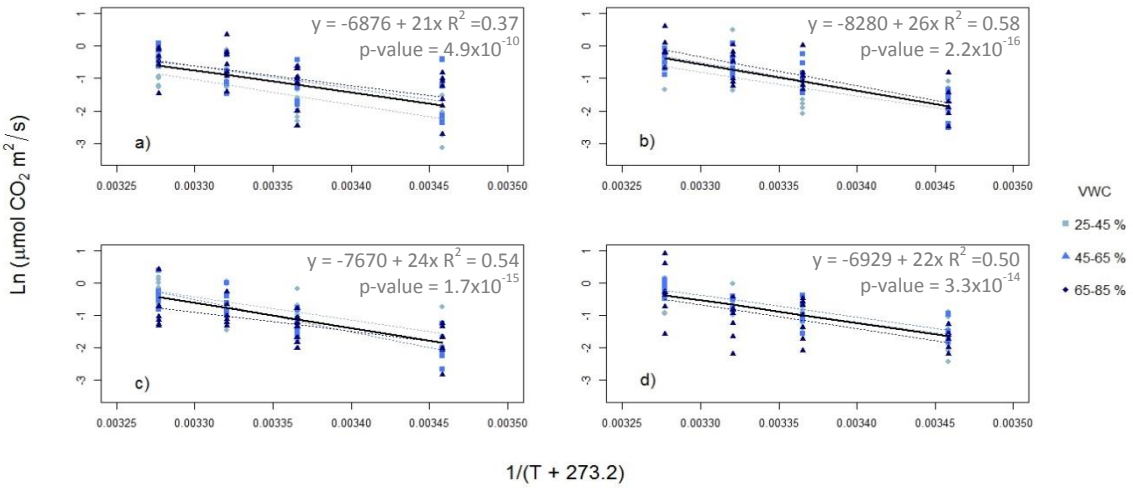


Figure 4.3 The natural logarithm of CO_2 fluxes (µmol / m^2 / s) from (a) abandoned banana; b) cultivated banana; c) mature forest; d) pasture) against the reciprocal of absolute temperature. The dashed coloured lines are simulating the individual moisture treatments with the Arrhenius model. The black solid line is simulating the overall data with the Arrhenius model (all moisture treatments combined).

4.4.2 Response of respiration to soil moisture

The response of soil temperature to moisture changes varies by land-use. High soil moisture content caused a significant decrease in soil respiration rates for the mature forest soils from 0.54 to 0.32 (µmol / m^2 / s) with M1 and M3 moisture treatments, respectively. The opposite effect was found on the other sites, with the abandoned banana producing a significant increase in CO_2 (from 0.29 to 0.49 (µmol / m^2 / s)) with increased moisture content (Figure 4.3). The highest mean rates of soil respiration were measured on the cultivated banana soils at the highest moisture treatment (60-80 %) (0.56 ± 0.41 µmol/m^2/s) with the lowest measured on the abandoned banana soils at the lowest moisture treatment (20-40 %) (0.29 ± 0.20 µmol/m^2/s), which was also significantly different to the other sites at this moisture treatment (Figure 4.4 and Appendix 3.1, Table 3.3 for full details of individual site regressions). Overall, the mean VWC for each moisture treatment between the sites was very similar with generally small standard errors (Table 4.4). However, on the mature forest there were a few cores that had a very high VWC, circled in red on figure 4.5 which went beyond the limits of the high moisture treatment range (60-80 %), due to initial errors when measuring VWC, when the soil cores first arrived. A linear regression was performed on the data with these cores removed and the same result was found, although this relationship was stronger without the cores present in the analysis (Appendix 3.1, Table 3.4).

Table 4.4 Mean VWC (%) with standard errors for each moisture treatment on the four sites

Site	M1	M2	M3
VC-AB	31.0 ± 2.5	49.0 ± 2.3	71.0 ± 3.2
VC-B	31.7 ± 1.6	53.9 ± 6.4	77.4 ± 2.1
VC-F	31.1 ± 1.5	48.8 ± 6.2	78.3 ± 9.5
VC-P	30.3 ± 1.6	50.4 ± 1.9	71.5 ± 1.7

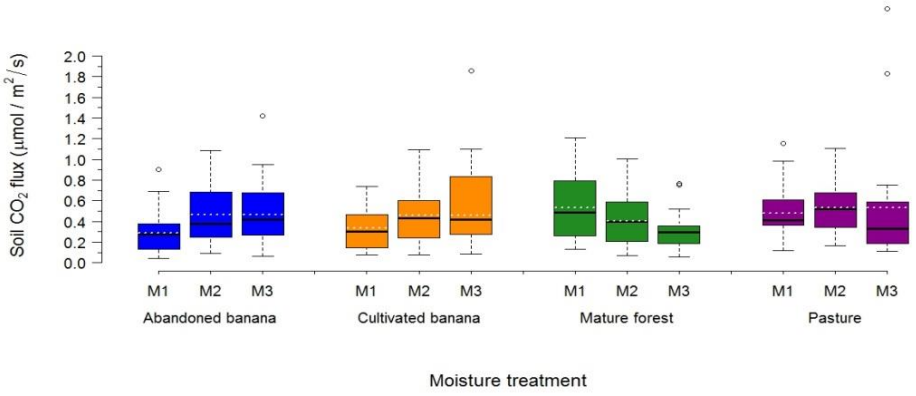


Figure 4.4 Mean CO_2 fluxes (µmol / m^2 / s) from the 24 day incubation experiment (n = 32 per site) at three different moisture treatments (M1 = 20-40 %, M2 = 40-60 %, M3 = 60-80 %) with soils (0-10 cm) from four different sites (abandoned banana = blue, cultivated banana = orange, mature forest = green, pasture = purple). Boxes enclose the interquartile range, whiskers show the full range. Dashed white lines represent the means and solid black lines represent the median values.

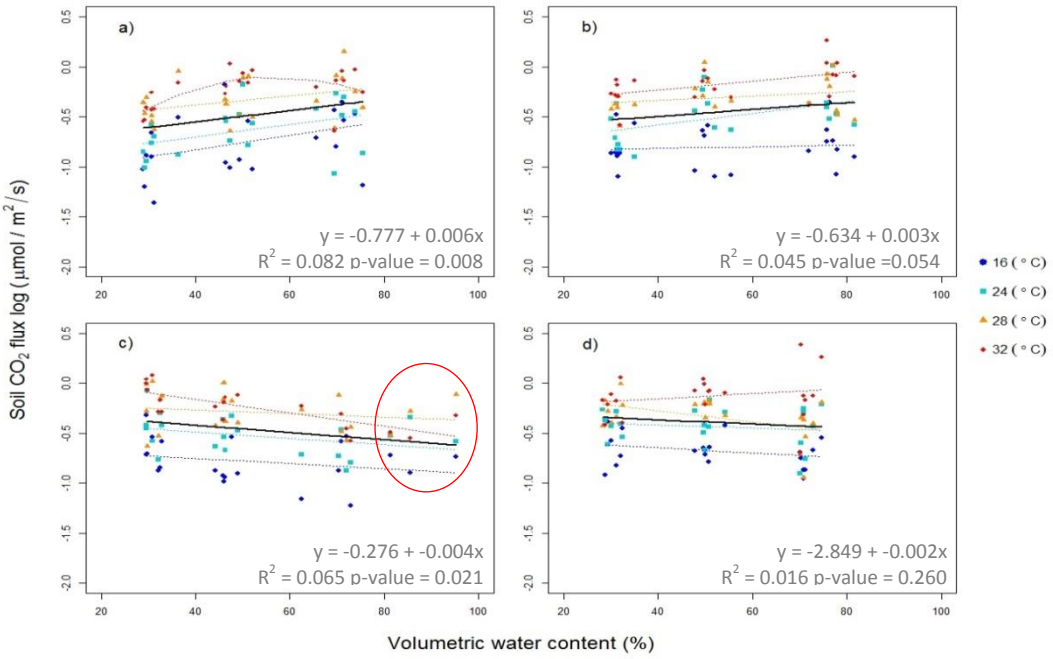


Figure 4.5 Linear and quadratic relationships between logged soil CO_2 flux (µmol / m^2 / s) and VWC under four temperatures (16 °C = dark blue, 24 °C = light blue, 28 °C = orange, 32 °C = red) on the four different soils (a) abandoned banana; b) cultivated banana; c) mature forest; d) pasture). The dashed coloured lines represent the linear regression for the individual temperatures. The black solid line represents the overall regression (all temperatures combined) with regression details in the bottom right corner for each site.

4.4.3 Combined effect of soil temperature and moisture on soil respiration

CO_2 fluxes on all the sites were significantly affected by increasing temperature, but the effects of moisture were inconsistent and varied by land-use or site (Figure 4.6). There were no significant temperature and moisture interactions for the pooled data, although synergistic effects were evident for individual site data. Mixed model analysis did indicate that there was a significant relationship between soil CO_2 flux and temperature (p-value = 2.2×10^{-16}), with temperature causing an increase in flux by approximately 0.039 ± 0.001 ($\mu mol/m^2/s$) for every °C increase in temperature. However, for the pooled data, soil moisture, time (number of days since the start of the experiment) and site had no significant effect on soil CO_2 flux (p-values = 0.50 and 0.22, respectively) (Table 4.5).

There was evidence of temperature and moisture interactions if the data were disaggregated by site. For example, abandoned banana soils had a significant relationship with temperature (p-value = 3.0×10^{-13}) causing an increase by approximately 0.034 ± 0.003 ($\mu mol/m^2/s$) for every °C increase in temperature. VWC also had a significant effect (p-value = 0.013), causing an increase in flux by 0.006 ± 0.002 ($\mu mol/m^2/s$) for every % increase in VWC (Table 4.5). Additionally, when looking at the individual temperature treatments separately, the relationship between CO_2 flux and VWC had a parabolic type relationship with a decrease in CO_2 flux after 65 % VWC (Figure 4.5). For cultivated banana soils, temperature was the only significant factor affecting fluxes (p-value = 2.2×10^{-16}), causing an increase of 0.040 ± 0.003 ($\mu mol/m^2/s$) for every °C increase in temperature. Respiration in mature forest soils, like abandoned banana was significantly affected by soil temperature and VWC (p-value = 2.2×10^{-16} and 0.012, respectively). Temperature caused an increase in CO_2 flux by 0.036 ± 0.003 ($\mu mol/m^2/s$) and VWC decreased CO_2 flux only very slightly by 0.003 ± 0.001 ($\mu mol/m^2/s$) for every % increase in VWC, which can be seen clearly among the water treatments in figure 6. Finally, on the pasture soils, temperature had a very significant effect but also, time had a weak effect on the CO_2 fluxes (p-value = 6.0×10^{-16} and 0.045, respectively) with temperature increasing the fluxes by 0.033 ± 0.003 ($\mu mol/m^2/s$) for every °C increase in temperature and time, decreasing fluxes by 0.006 ± 0.002 ($\mu mol/m^2/s$).

Table 4.5 Mixed model relationships between soil CO_2 flux with soil VWC, temperature and time. Significant code * = P< 0.05

Site	Treatment	Chi squared	P-value	Intercept	Slope
V - F	Temperature: VWC	1.14	0.29		
	Temperature	69.79	2.2×10^{-16} *	-1.186 ± 0.107	0.036 ± 0.003
	VWC	6.36	0.01 *		-0.003 ± 0.001
	Time	0.59	0.44		
V - B	Temperature: VWC	1.37	0.24		
	Temperature	93.83	2.2×10^{-16} *	-1.461± 0.076	0.040 ± 0.003
	VWC	3.11	0.08		
	Time	1.55	0.21		
V - AB	Temperature: VWC	0.61	0.43		
	Temperature	53.21	3.0×10^{-13} *	-1.628 ± 0.147	0.034 ± 0.003
	VWC	6.17	0.01 *		0.006 ± 0.002
	Time	2.18	0.14		
V - P	Temperature: VWC	1.20	0.27		
	Temperature	65.47	6.0×10^{-16} *	-1.138 ± 0.091	0.033 ± 0.003
	VWC	1.00	0.32		
	Time	4.01	0.045 *		-0.006 ± 0.003
All data	Temperature: VWC	0.02	0.90		
	Temperature	237.72	2.2×10^{-16} *	-1.346 ± 0.044	0.036 ± 0.002
	VWC	0.48	0.50		
	Time	4.47	0.22		
	Site	2.62	0.11		

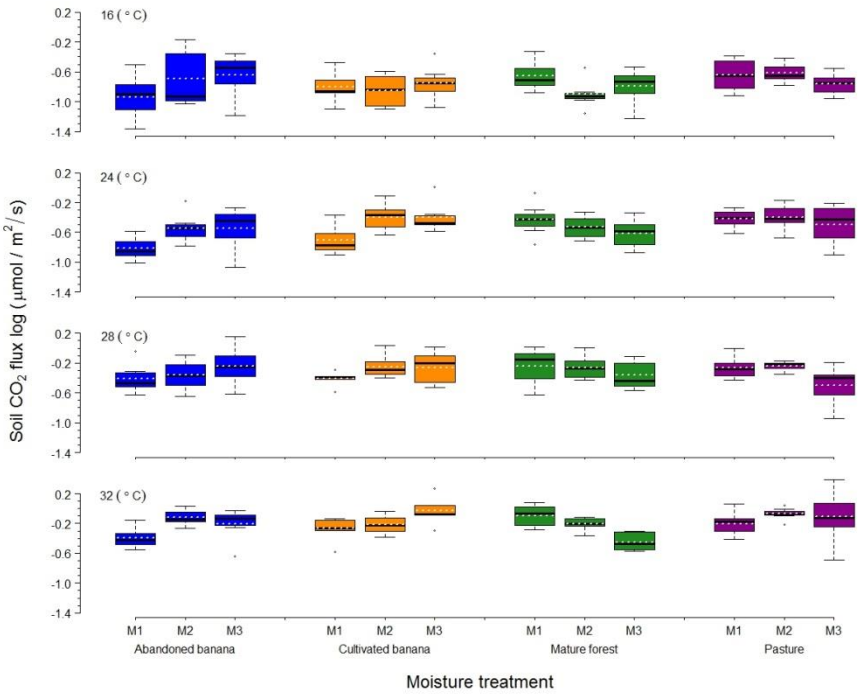


Figure 4.6 Mean CO_2 fluxes (µmol / m^2 / s) from the 24 day incubation experiment (n = 28 per site) for three moisture treatments (M1 = 20-40 %, M2 = 40-60 %, M3 = 60-80 %) under four temperatures (16 °C, 24 °C, 28 °C, 32 °C) with soils (0-10 cm) from four different sites (abandoned banana = blue, cultivated banana = orange, mature forest = green, pasture = purple). Boxes enclose the interquartile range, whiskers show the full range. Dashed white lines represent the means and solid black lines represent the median values.

4.5 Discussion

4.5.1 Soils from different land-uses share a common response to temperature

Consistent with expectation, temperature was a good controller of soil heterotrophic respiration with similar response curves for all the sites, suggesting that it may be simple to model soil temperature responses in these ecosystems. There was no evidence of the fluxes decreasing at the higher end of the temperature spectrum, which may have been because the highest temperature used in this incubation study was 35 °C and many enzymes only begin to degrade at or above 45 °C (Wallenstein et al., 2011). These findings are in keeping with other tropical soil incubation (Bekku et al., 2003; Holland et al., 2000; Balser and Wixon, 2009; Wood and Silver, 2012) and field studies (Doff Sotta et al., 2004; Salinas et al., 2011).

In comparison to the observational field study carried out in 2011 on the same soils (Chapter 3, Table 3.4 & Figure 3.4), there was a difference in soil respiration and temperature relationships. In situ CO_2 flux was only correlated with soil or air temperature for the pasture soils. This may be a reflection of the many other confounding variables that influence soil respiration in space and time and the presence of roots which may have different temperature responses.

4.5.2 The effects of soil moisture on soil respiration vary with land-use

Contrary to expectations, soil moisture was consistently a poor controller of soil respiration. This is interesting because the common assumption is that soil moisture is one of the more dominant controls on soil respiration in the tropics (Butterbach-Bahl et al., 2004; Vasconcelos et al., 2004; Werner et al., 2006; Holtgrieve et al., 2006). However, research over the last decade has highlighted the complexity of this relationship (Gabriel and Kellman, 2011; Rodrigo et al., 1997) within and across tropical forests, with mixed responses to in-situ through fall studies (Wieder et al., 2009; Wood and Silver, 2012; Cleveland et al., 2010) and controlled laboratory experiments (Cleveland et al., 2010; Davidson et al., 2004; Sotta et al., 2007; Metcalfe et al., 2007). In our study, we found that the response of heterotrophic respiration fluxes to changes in soil moisture was dependent on cover type.

Moisture availability on the mature forest soils had a significant relationship with soil respiration, with 60-80 % VWC decreasing CO_2 fluxes by 40 % compared to when at 20-40 % VWC. Other tropical studies have also reported this type of relationship when soil moisture concentrations above field capacity or increased rainfall have caused a suppression of microbial organic matter decomposition (Cleveland et al., 2010; Chambers et al., 2004). This was primarily explained by the simultaneous decrease in O_2 concentrations in the soils (Silver et al., 1999), which occur due to the slowing down of diffusion rates of gasses in water compared to when in air and even when the pores are not fully saturated, the area for diffusive movement decreases (Skopp et al., 1990; Luo and Zhou, 2010). O_2 is such a critical part of the redox reactions controlling microbial respiration, due to its role as an energetically favourable electron acceptor (Hall et al., 2013), that a lack of O_2 can cause a considerable decrease in soil respiration. On the other hand, the high CO_2 fluxes that were found on the drier soils could be a reflection of O_2 increases in the micro pores and stimulating aerobic decomposition (Silver et al., 1999; Schuur et al., 2001). Furthermore, (Cleveland et al., 2010) suggested that the decline they saw in CO_2 fluxes under wet conditions could have also been a result of diluting dissolved organic matter (DOC), which is a key substrate and energy source for many heterotrophic microorganisms. These soils are sandy loam (sand = 60; silt = 36; clay = 4) with high organic matter content (Harris, 1981; Schjønning et al., 2003), which are both conducive to creating good aeration and drainage to deeper soil layer. However, this does not seem to be the case in our experiment. One potential reason for this could be having cores that are 10 cm deep and so the natural effect of drainage to deeper layers is constrained.

In contrast to the mature forest, soil moisture had the opposite effect in both the abandoned banana and cultivated banana soils with an increase in soil respiration under high soil moisture concentrations. This was principally seen between the lowest (M1) and intermediate (M2) soil moisture treatments with the fluxes plateauing at the highest moisture content (M3), which can be explained by dry conditions inducing dormancy or spore formation in soil microorganisms and cell dehydration (Stark and Firestone, 1995) in some soils. During drier periods, the mobility of microorganisms and diffusion of soluble organic C substrates may also be reduced, impeding organic matter decomposition.

The response of pasture soils to variations in soil moisture was different again; we found no significant relationship between soil water content and soil respiration, except perhaps a weak indication of the highest fluxes occurring at intermediate water contents. The pasture soils had the highest measured respiration rates compared to any of the other soils and yet contain the lowest total C content and smallest proportion of labile C. However, pasture soils contain a large amount of small roots, a large proportion of which could be dead, resulting in high decomposition rates and offsetting any moisture related effects on soil respiration (Silver et al., 2005). There may also be the influence of a less anaerobic soil environment in the soil pores due to the high proportion of sand in this sandy loam (sand = 62; silt = 36; clay = 3).

Research on bacterial communities after conversion from rainforest to pasture found that pasture sites have a more homogenized bacterial community (Rodrigues et al., 2013) and it might be easier for these particular microorganisms to adapt to water stress. In the field, the pasture site has a microclimate that is less humid and experiences more extremes of flooding and drought, which would allow the bacteria to possess the osmoregulatory adaptation for survival under a wide spectrum of soil water environments (Harris, 1981), undergoing extreme downshock (plasmolytic) and upshock (plasmoptic). (Orchard and Cook, 1983), suggested that fungi can tolerate water stress better than bacteria, which might explain the resilience to extreme water content if a large proportion of fungi were present, this is a hypothesis that needs to be addressed and these findings could be the basis for future work.

The CO_2 fluxes from the soil moisture experiment responded to water availability in a similar way as the in-situ field observations (Chapter 3, Table 3.4 & Figure 3.4), where soil respiration from abandoned banana and mature forest soils were affected by soil moisture content. The field data showed that this ecosystem was not necessarily defined as having a wet and dry season, as would be expected from a tropical forest (mean soil VWC for dry season was 45 % and wet season 49 %). However, the minimum and maximum soil VWC experienced over a year ranged from 26 % to 56 %.

4.5.3 Increasing sensitivity of respiration to soil moisture at high temperatures

When isolating the effects of temperature and moisture separately, temperature significantly increased soil respiration on all the sites and moisture had a significant effect on the abandoned banana and mature forest soils. However, small differences in how the sites responded to the moisture treatments at each temperature were observed. Respiration rates on the abandoned banana soils increased with temperature and water treatment, except at 32 °C, when the flux rates plateaued at the highest moisture treatment, implying that respiration on these soils is sensitive to high moisture at increased temperatures. This has been seen in a tall grass prairie where soil respiration was more sensitive to temperature change in wet soil rather than dry (Harper et al., 2005) Although soil respiration was not significantly affected by moisture on the cultivated banana soils, there was a clear lack of moisture response at the lowest temperature, which then sharply rose when at 24°C with increased water availability. This affirms the theory that soil respiration usually responds to the most limiting factor; when soil moisture is low, temperature sensitivity is reduced (Carlyle and Than, 1988). The mature forest had the most interesting pattern of soil respiration relationships with soil temperature and moisture. Temperature caused a significant increase in soil respiration, while VWC had a decreasing effect, which was very pronounced at 32 °C. This has also been seen in a through fall exclusion experiment on humid tropical soils in Puerto Rico where soil moisture availability constrained the positive effect of temperature (Wood et al., 2013). The pasture soils had high respiration rates at M1 and M2 for all four temperatures but then decreased with M3 regardless of the temperature, especially when at 28 °C. These soils also had a very slight time effect which may be due to a lack of fresh material during the incubation and fast turnover rates that are normally experienced in the field.

Temperature sensitivity linked to substrate and water availability

The $\boldsymbol{Q_{10}}$ estimate for the mature forest in this study was 3.24 at 24:28 °C. This is similar to reported $\boldsymbol{Q_{10}}$ values from a soil core translocation field study in the same region in Peru, where $\boldsymbol{Q_{10}}$ values of 2.94 were reported from soils at an elevation of 1000 m a.s.l (average temperature of 21.6 °C) and 6.29 at an elevation of 200 m a.s.l (average temperature of 26.4 °C) (Zimmermann et al., 2010b). Similarly, in a

Brazilian tropical forest study the estimates of $\boldsymbol{Q_{10}}$ were 2.37 (Holland et al., 2000) and (Mo et al., 2007) found $\boldsymbol{Q_{10}}$ values of approximately 2.3 for a monsoon forest in China. The $\boldsymbol{Q_{10}}$ results from this incubation study had very large standard deviations, making it difficult to elucidate the overall patterns between the temperature and moisture treatments. The general pattern for all the sites was a decrease at the lower and higher temperatures, suggesting that the soils became less sensitive to temperature when incubated at higher and lower temperatures, an outcome consistent with other studies (Holland et al., 2000; Zimmermann et al., 2009b; Lloyd and Taylor, 1994; Kirschbaum, 1995). However, this is contrary to a Malaysian tropical soil study where cooling from 24 to 16 °C led to an increase in $\boldsymbol{Q_{10}}$ from 2.1 to 2.7 and an increase in temperature had no effect (Bekku et al., 2003). In a broadleaf evergreen forest in China, temperature sensitivities were reduced at lower moisture levels (Zhou et al., 2014), whereas, in a tropical soil study in Peru by (Zimmermann et al., 2010b; Zimmermann et al., 2010a), lower temperature sensitivities were found with increased moisture availability. This was not noticeable on our soils due to the large standard deviations.

Theory suggests that complex molecules have low decomposition rates and high activation energies, which result in high intrinsic temperature sensitivities. Lower temperature sensitivities may be measured when certain environmental conditions are constrained, e.g. when moisture or substrate availability are limiting; this is known as the 'apparent' temperature sensitivity (Davidson and Janssens, 2006; Bosatta and Ågren, 1999). The highest activation energy was found on the cultivated banana soils (69 kJ mol^{-1}), which increased with higher moisture content. These soils had significantly lower bulk C content (8.4 Mg C ha^{-1}) compared to the mature forest (17.6 Mg C ha^{-1}) and abandoned banana soils (16.4 Mg C ha^{-1}) and a relatively thin organic layer. Although the proportion of labile material in these soils was similar to the mature forest (Chapter 2, Table 2.5), the absolute amount of labile C was less, potentially leading to higher apparent activation energy because soil microbes had a smaller pool of labile material to utilise. The mature forest also had a high activation energy (64 kJ mol^{-1}) and the overall highest compared to the other sites when at the M2 moisture treatment (82 kJ mol^{-1}), which was similar to reported values of a study based in Scotland where forest soils had an activation energy of (83 kJ mol^{-1}) (Fang et al., 2005). This may be a reflection of the substrate, rather than a limited supply of C, with forest soils containing more recalcitrant or complex substrates (e.g. lignin, aromatic compounds and plant defensive compounds)

that are harder to decompose. The pasture soils had similar activation energies with all three moisture treatments (58 kJ mol^{-1}).

4.6 Conclusions

The majority of soil temperature and moisture sensitivity studies are based in high latitudes (Oelbermann et al., 2008) and boreal forests (Niinistö et al., 2011) with insufficient reference to topical regions, yet tropical soils are an important part of the global C cycle. The studies that are based in the tropics have mostly focused on soil warming or drought and very few included the interaction of soil moisture, temperature and soil respiration, even less so in reference to different land-uses. Predictions of soil organic matter response to ongoing deforestation, climate and land-use changes have been marred by inconsistency and uncertainty arising from the complexity of soil respiration drivers.

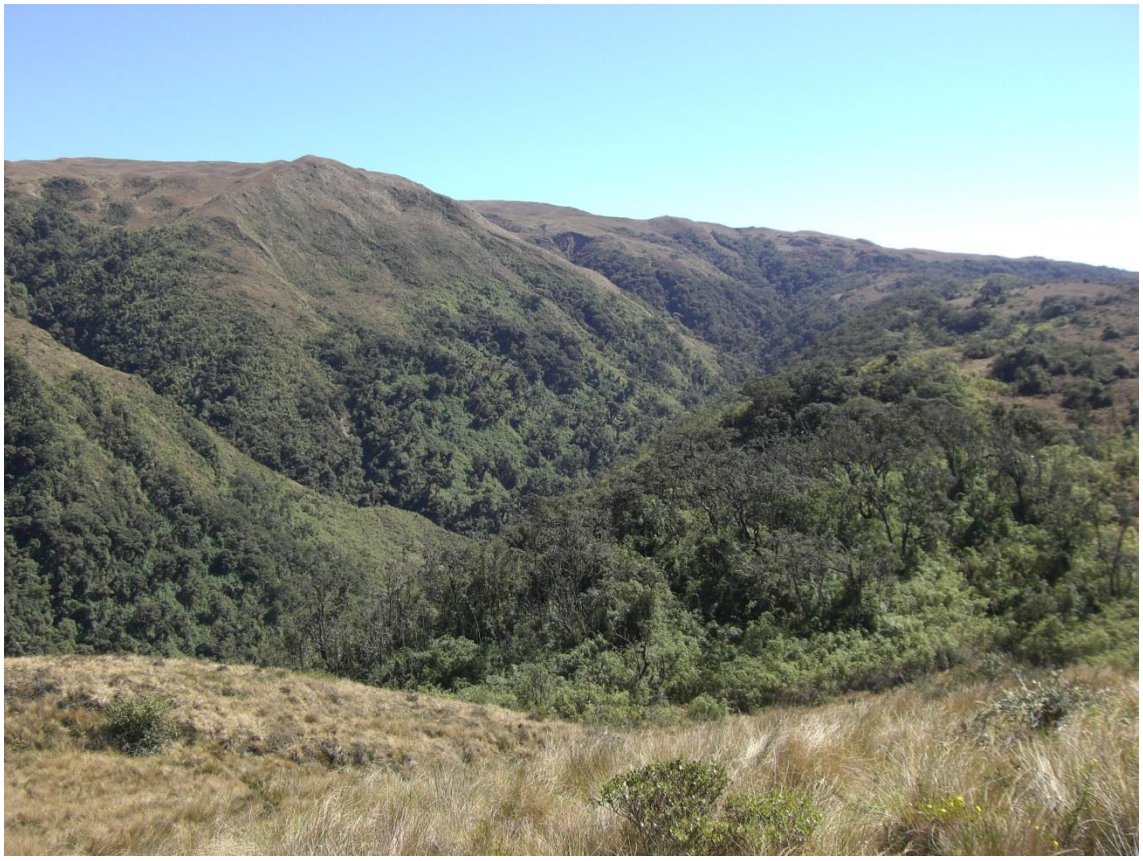
This study was the extension of year-long observational soil respiration measurements taken from an abandoned banana, pasture and mature forest site in the Peruvian tropical forests, where significant relationships were found between soil temperature, VWC and CO_2 efflux. In order to examine and compare the soil moisture and temperature response in controlled conditions, where there are no other variables influencing the response to field manipulation experiments, we conducted a short-term incubation experiment on intact cores from the same sites as the field study.

The outcome affirmed but also challenged pre-conceptions of what is controlling soil respiration. Our results suggest that the normally recognised exponential relationship between temperature and soil respiration is not explicit and that soil moisture causes the temperature effect to weaken at higher moisture levels in organic rich forest soils. Furthermore, our results show that the response of heterotrophic respiration to changes in soil moisture is also dependent on cover type, highlighting the fact that land-use history too plays a crucial role.

In our experiment, soil respiration emerges as an individual process subject to many variables in environmental drivers both within and among sites and in conflict with any generalization or theory. This points towards the need to focus further research on how these variables interactively affect soil heterotrophic respiration, on the relationships between the drivers of soil respiration, on the influence of soil moisture and temperature on different C pools and clarity on how soil texture influences soil respiration in tropical ecosystems.

~ Chapter 5 ~

Synthesis and conclusions



Tropical montane grassland and montane cloud forest transition in the Peruvian Andes.

5.1 Key findings

This section synthesises the scope, process and results of the research by bringing together the soil C dynamics of the key study sites and by answering the questions put forward at the beginning of the thesis (Chapter 1, Section 1.7). The answers are necessarily provisional and tentative in view of the gaps in the general database; nevertheless, they represent considerable progress in an area where little knowledge has been accumulated to date.

Q1. Does soil C storage alter under different land-uses?

Land management in the montane grasslands did not significantly affect total soil C stocks, however, the synergistic effect of burning and grazing reduced the proportion of free LF (from 30.0 ± 5.7 in the control to 14 ± 5.3 %) and the effect of burning alone increased the abundance of C in the occluded LFs (from 5.2 ± 0.8 in the control to 12.0 ± 2.5 %). Collectively, total soil C stocks on the sites measured in the montane cloud forest were unaffected by burning in the last 10 years.

At the premontane elevation, the loss of total soil C content was dependent on the type of agricultural land-use. Secondary forest succession, selective logging, abandoned banana plantation and abandoned pasture allowed soils to recovery back to C stocks similar to the mature forest (~ 25 Mg C ha^{-1}). The pineapple plantation soils had no net change in total C stocks, but there was a reduction in the free and occluded LFs (from 12.1 ± 2.6 in the control to 2.8 ± 0.1 %), possibly attributable to easily decomposing plant leaf material. The cultivated banana soils had significantly lower total soil C stocks (16.3 ± 0.5 Mg C ha^{-1}) and the distribution of C within the soil was altered, with higher proportions of occluded F (from 12.4 ± 3.0 in the control to 26.4 ± 3.1 %). Although there were no significant C losses in the heavy F, there was ~ 16 % less C in this fraction, which probably caused the reduction in total C content. The low intensity grazed soil was dominated by grass derived C and had significantly lower total soil C stocks (19.1 Mg C ha^{-1}) and a decrease in the free LF (6.8 %), whereas the other pasture sites were predominantly made of forest derived C, a more recalcitrant material, which may have resulted in the higher total C stocks (28.4 and 36.1 Mg C ha^{-1}).

An important finding from this study was that even when the total C stocks appeared to be unaffected, the distribution of C storage within the soils changed with some land-uses.

Q2. What are the soil CO_2 emissions associated with land-use?

In the montane grasslands, the combination of burning and grazing increased soil carbon emissions by 33 %, whereas, individually there were no significant changes to soil CO_2 fluxes (grazed = 0.95 ± 0.05 and burnt = 0.88 ± 0.05 umol m^{-2} s^{-1}). Faster decomposition rates (used as a proxy for microbial decomposition) were only detected on the grazed plots at Wayqecha, where CO_2 fluxes were generally higher and temperatures warmer. In the montane forest, there were no net changes in soil CO_2 fluxes or decomposition rates. In the premontane elevation, the low intensity grazed pasture soils had a significant increase in soil C emissions (from 2.76 ± 0.30 in the control to 6.24 ± 0.44 umol m^{-2} s^{-1}). Even though partitioning respiration was not feasible, decomposition data indicates very fast rates of SOM decomposition and natural abundance isotope data show a dominance of grass derived C, which is easily decomposed, hence the increase in CO_2 is probably due to microbial decomposition, rather than root respiration. The other land-uses measured had similar CO_2 fluxes to the mature forest (~ 3 umol m^{-2} s^{-1}).

Soil respiration and decomposition rates are good predictors of soil C loss on pasture and montane grassland soils, with significantly higher CO_2 fluxes (**Q2**) measured on sites with significant losses of either total soil C or free LF (**Q1**), suggesting that CO_2 emissions were a result of increased decomposition of SOM, rather than root respiration The exception to this rule was on the cultivated banana soils where decreased total soil C did not result from increased C losses to the atmosphere, despite relatively fast decomposition rates.

Q3. Do the drivers of soil organic matter decomposition alter under different land-uses?

Soil and air temperature were the main drivers of soil respiration in the montane grasslands, but the combination of burning and grazing diminished the magnitude of this driver. In the montane forest, soil respiration was significantly related to time of year and air temperature and burning did not alter this relationship. In the premontane elevation, soil moisture was the dominant driver in the mature forest and

abandoned banana but this changed to temperature in all other land-uses, with the exception of the cultivated banana site where the factors measured in this study did not explain variability in fluxes.

The incubation experiment confirmed how important soil moisture is to organic matter decomposition in mature forest soils, with high moisture content becoming the dominant factor at higher temperatures and decreasing soil respiration. This finding was site specific, with the abandoned banana and pasture soils showing the opposite trend.

Even when there are no net changes in soil CO_2 fluxes (Q2), the environmental drivers of soil respiration can change under different land-uses (Q3).

The synergistic relationship between soil moisture and temperature alter under different land-uses (Q3).

Site specific differences:

The plots at Wayqecha in both the montane grassland and montane forest were more influenced by anthropogenic land management than those at Acjanaco. For example, the forest soils had a 50 % loss of C in the surface layers of the soil compared to the 13 % and 20 % losses at Sunchubamba and Acjanaco. The decomposition rates and soil CO_2 fluxes were also much greater on the burnt and grazed montane grasslands plots at Wayqecha (Wayqecha = 1.88 ± 0.23 and Acjanaco = 0.82 ± 0.05 umol m^{-2} s^{-1}). This may have been due to the slightly warmer temperatures at this site, the intensity of the fire, or this site being more susceptible to erosion.

Elevational differences:

The mature forest soils had much smaller total C content (28 ± 2 Mg C ha^{-1}) and higher soil CO_2 fluxes (2.8 ± 0.3 umol m^{-2} s^{-1}) than in the montane forest (162 ± 36 Mg C ha^{-1} and 1.5 ± 0.1 umol m^{-2} s^{-1}) and montane grassland (142 ± 17 Mg C ha^{-1} and 0.9 ± 0.1 umol m^{-2} s^{-1}). There was also consistency in the lack of changes to soil C dynamics with the influence of burning in the cloud forest, whereas, the activities taking place in the premontane elevation appeared to be more susceptible to C losses.

5.2 Summary and comparison to other studies

In order to compare the key findings from this study to other studies in the tropics and higher latitudes, the sites at the premontane elevation have been aggregated into three broad categories (agriculture, pasture and secondary forests) and the different burning years in the higher elevations, averaged. This has reduced the number of sites observed from 23 to 10. Figure 5.1 illustrates these results with errors reported.

The conversion from primary forest to agriculture at the premontane elevation caused a 26 ± 24 % loss of SOC, which is in keeping with three meta-analysis review papers, where losses of 13 % (Guo and Gifford, 2002), 20-30 % (Murty et al., 2002) and 25 % (Don et al., 2011) have been reported. Typically, greater losses have been measured in tropical and temperate regions compared to boreal and the degree of SOC loss is generally dependent on the type of crop measured (Wei et al., 2014). Conversion from primary forest to pasture caused a SOC loss of 14 ± 15 %. Disparate results are very common among pasture studies, with losses of 73 % and gains of 51 %, based on 93 studies worldwide (Don et al., 2011).

Some studies have found that SOC losses are partly reversible when agricultural practices are left abandoned. In this study, the secondary forest included an abandoned banana plantation, rice plantation and a forest which had experienced previous logging. Compared to the agricultural sites (banana and pineapple), there were signs of recovery and on average an increase in SOC stocks. Based on 20 studies, meta-analysis review papers report losses of up 64 % and gains of 72 % (Don et al., 2011). In this study, losses were 22 ± 7 %.

Very few papers have looked at the effect of SOC stocks with grazing and burning at higher tropical elevations. Land management in the Puna showed both losses and gains measured in SOC stocks (- 32 to +13 %), this is why the errors are so large when grouping the data together and can be primarily explain by the different temperatures that were observed between the sites. Burning in the montane cloud forest caused a reduction in SOC stocks between 10 and 46 % but some studies have reported losses of up 90 % (Gibbon et al., 2010; Román-Cuesta et al., 2011; Fearnside, 2000; Asbjornsen and Wickel, 2009). This

highlights the extreme heterogeneity of soils in this ecosystem and the recovery time since burning and intensities.

There was a clear trend of decreasing SOC stocks at lower elevations, which coincided with increasing soil CO_2 fluxes. This result is consistent with other montane studies (Girardin et al., 2010; Zimmermann et al., 2009b). However, the large errors associated with the losses in SOC make it difficult to generalise whether one elevation is more susceptible to changes than another. Making broad statements about the effects of so many land uses would be haphazard and this study reinforces the need to further investigate the complexities of these ecosystems.

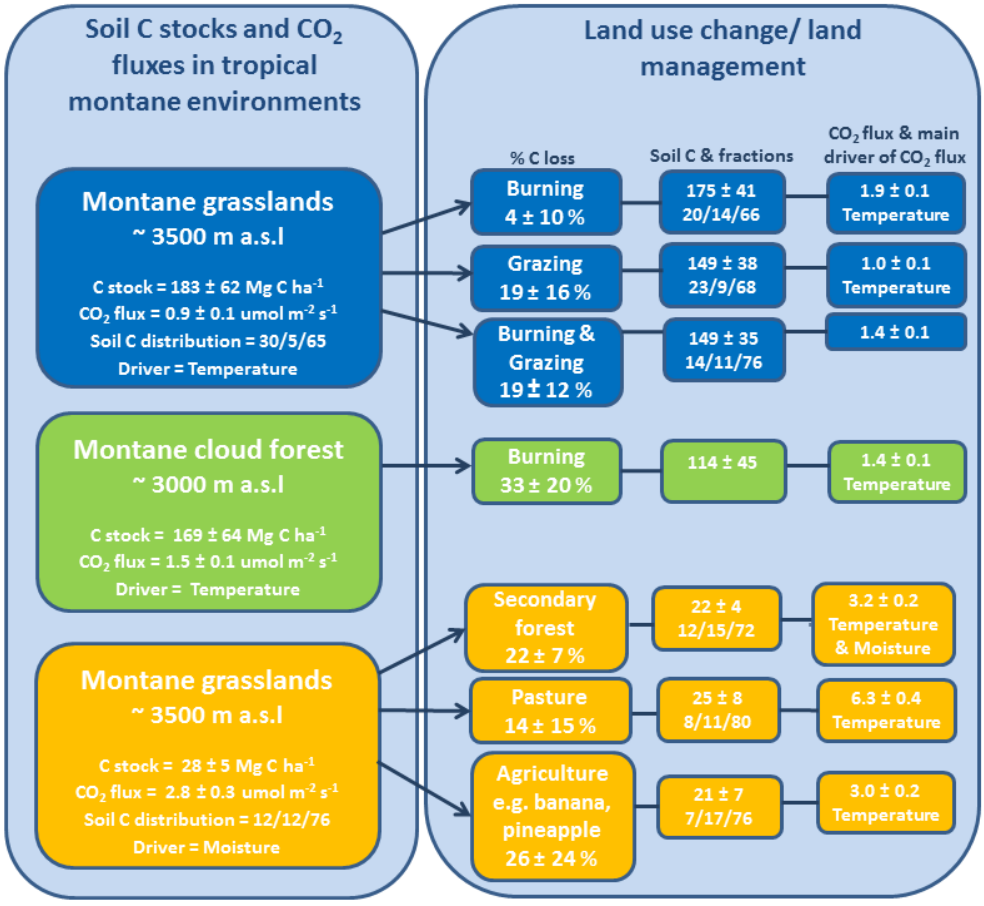


Figure 5.1 Soil C stocks and CO_2 fluxes in tropical montane environments under land-use/land management. The distribution of C within the soil matrix is represented as: free LF/occluded LF/ heavy F. All C stocks are a sum of 0-30 cm in Mg C ha^{-1} and CO_2 fluxes are the mean annual flux in umol m^{-2} s^{-1}. The 'driver' indicates the significant environmental variable associated to the CO_2 fluxes. All values are given with 1 standard deviation of the mean.

5.3 End-users

The results from this study have shown some interesting and new insights into how SOC storage is affected in managed Tropical Andean environments, but collecting enough data to provide a full inventory of SOC stocks and CO_2 fluxes for a whole region is virtually impossible. However, this type of data is relevant for both inventory-based estimates and process-based models, which are used by International Environmental Policy Programmes (e.g. the Kyoto Protocol, Article 4 of the United Nationals Framework Convention on Climate Change and the International Panel on Climate Change), as part of periodic updates and published national inventories, needed to assess anthropogenic emissions and sinks of greenhouse gasses (UNFCCC, 1994). These biogeochemical models are very useful tools for advancing our understanding of the drivers of SOC changes under different managements and climates by upscaling current and future SOC stock changes and allowing for the integration of processes (van Wesemael et al., 2010).

Reducing emission from deforestation and forest degradation (REDD), is a framework that allows financial rewards in developing countries for any reductions in CO_2 emissions, but it can only be successful with an accurate quantification of SOC stocks under land-use change and management. By combining the data from a broad range of different land-uses in varying ecosystems, such as the one in this study, with inventory and process based models, policymakers can make informed decisions on which types of land-uses can slow, halt or even reserve the losses of SOC after deforestation.

5.3.1 Inventory based estimates

Inventory methods are based on ground measurements from published ecological literature and statistics on forestry and agriculture. The data includes per-hectare changes in SOC stocks following changes in land-use and when combined with data on land-use change rates, using satellite images and remote sensing data, empirical bookkeeping models can be used to track the changes in C. Bookkeeping models have been used for many years (Houghton et al., 1983) and when applied with geographical information systems (GIS), annual CO_2 emissions and SOC stocks can be calculated at regional, national and even global scales. However, extensive data are limited for tropical ecosystems compared to temperate regions

and there is considerable uncertainty; partly because of the spatial variability in soils and microclimate but also the extent and time since disturbance (Kutsch et al., 2009).

5.3.1 Modelled estimates

Process-based ecosystem models use climatic drivers and other environmental factors to calculate C densities in different types of ecosystems. The most common and widely used ecosystem based models are RothC Rothamsted Carbon Model (Coleman and Jenkinson, 1996); Century (Parton et al., 1988); DNDC (Li et al., 1994) and SOCCRATES (Lloyd et al., 1995). Compared to bookkeeping models, these models can reflect much greater spatial and temporal variability in C density and responses to environmental conditions from biome level to global scales. In order to estimate and predict future changes in SOC stocks for a particular location or management scenario, some of the driving parameters included in models are: plant functional types; soil C pools (e.g. fast and slow decaying fractions of SOM); soil particle sizes; topographic position; climate data and land management information (Watson et al., 2000). The simulated SOC stocks also describe the transformation, protection and mineralisation of SOM, with different dependencies on environmental conditions. However, these models require high data input and their modelled SOC stocks can be markedly different from field observations.

5.4 Broader implications

By the end of the 21st Century, the tropics are predicted to be approximately 5 °C warmer and experience 2 mm more precipitation per year (IPCC, 2014; Urrutia and Vuille, 2009). While this is less than in higher latitudes, the effect is of more imminent concern in tropical regions, with changes expected to take place faster than other ecosystems (Mora et al., 2013). The results of this study imply that the combination of these impending temperature increases and the current fast rates of deforestation and land-cover changes in the tropics could further accelerate the already increasing CO_2 emissions. This is because one of the key findings was a change in the drivers of SOM decompostion, from a moisture driven response to a temperature one, under both agricultural and pasture land-uses at the Premontane elevation.

5.5 Strategies for improving SOC stocks

5.5.1 Andean fire management

The predicted rising temperatures and changes to hydrological properties in Andean mountain ecosystems are likely to increase the spread of fires from managed grasslands (Puna) to adjacent montane cloud forests. Incentives to prevent fires from encroaching into montane cloud forests in Peru and Southern Ecuador have already started (Knoke et al., 2009; Román-Cuesta et al., 2011). These include the improvement of fire research, adaptive fire management and land-use diversification as an economic alternative. Mechanisms such as REDD, promote landowner participation into conservation activities by encouraging reforestation of degraded lands with green fire breaks to prevent the spread of fire. Farm-level diversification with reforestation of unproductive "wastelands" using economically valuable Andean plant species can provide a sustainable land-use system, which addresses the subsistence needs of local and indigenous communities (Knoke et al., 2009).

5.5.2 Premontane agricultural land management

The findings from this study suggest that montane environments may be more susceptible to losing C from the agricultural practices that take place there and that C sequestration is possible with secondary forest succession. To suggest that agriculture should be drastically minimised is unrealistic and rather a more appropriate management strategy should be suggested for the future of this region in light of the results obtained.

Soil C is a resource that can potentially be managed, particularly in agricultural lands where loss of SOC can be slowed or even reversed using various techniques (Victoria et al., 2012; Trumbore et al., 1995). This can be achieved by improving agricultural methods and productivity, which in turn reduces the need to cut down additional forest land. A few techniques have been proven to increase SOC stocks and soil fertility, including: the addition of animal manure or crop residues (mulching) (Bajorienė et al., 2013); the integration of several crops (Cambardella and Elliott, 1993); practice of agroforestry (Lal, 2004) and reduced tillage (Powlson et al., 2012). Another method is to choose highly productive crops or types of land-use. For example, the results from this study showed that although the CO_2 fluxes were highest on

the pasture soils, the loss of SOC stocks were ~ 12 % less than the agricultural practices. Fast decompostion rates on these pasture soils suggest that a considerable amount of respiration must have come from the roots and that these systems have a higher capacity for C storage.

5.6 Strengths and weaknesses of the sampling strategy

Absolute conclusions from a study such as this one would only be possible after substantial replication in the same type of land-use and history of land management over a new elevation gradient and for a longer period of measurement. This is no easy task, since finding a site with exactly the same land-use history is almost impossible in these hillsides. Also, the cost and time needed to sample and process samples from additional sites was not feasible within the timescale and budget of this project. Nevertheless, the strength of this study lies in the high level of in-site replication and a focus on process detail. Many variables were measured within each site in order to identify changes in soil C stocks and drivers of these changes. This included measuring: soil SOC stocks, density C fractions, pH, bulk density and particle size all at multiple depths and soil respiration, decomposition rates, temperature, moisture and further exploration of the soil moisture and temperature relationship with respiration. So, although spatial variability was lacking, especially in the premontane elevation band, the high level of heterogeneity found naturally within soils was accounted for within each site. In order to optimise the outcome of this study, all sites within each elevation band were chosen relatively close together. The purpose of this was to avoid other controlling factors, such as: geology, microclimate, slope, aspect and distance to rivers.

The most unique and valuable feature of this study is the wide range of sites that were investigated on a 2600 m elevation gradient, which accounted for the main anthropogenic activities occurring in this region. This has covered knowledge gaps in our understanding of how these ecosystems respond to altered land-use. Although challenging, this has allowed for observations of not only land-use changes but also how drivers of CO_2 alter with elevation and how they respond to differences in land management. This has provided a framework for other studies to continue with further replication and focus on the sites that have shown the largest C losses and greatest sensitivity to temperature and moisture.

5.7 Further research

This study has set the groundwork for a number of future investigations and analytical methods including: further replication of the land-uses studied, partitioning of soil respiration, microbial analysis, ^{14}C modelling, ^{13}C nuclear magnetic resonance spectroscopy and a greater depth of soil analysis.

5.7.1 A broader analytical basis

The drivers of soil respiration changed with certain land uses in this study and in some cases, the measured factors did not always explain variability in soil respiration. In order to fully understand why these changes have taken place, there are two very important questions that need to be addressed: (1) what is the contribution of root respiration (Ra) and SOM decomposition (Rh) to total soil respiration? (2) Do the microbial communities change under different land uses? PM- what about better constrained temperature and H2O responses first (your replication point)

Firstly, previous studies have found that the two components of soil respiration (Ra and Rh), respond to environmental conditions in unique ways and on different timescales (Dawson et al., 2002). For example, an increase in Ra respiration can be a reflection of increasing C inputs to the soil through photosynthesis and although it may significantly contribute to the net CO_2 flux, it has no effect on long term C storage in the soil (Kuzyakov, 2006), whereas, a decrease in Rh) respiration could imply that the potential for soil C storage has been reduced (Malhi and Grace, 2000). An attempt to separate Ra and Rh was made during the course of this study through both the manual removal of roots and a natural abundance isotope method, which utilises the difference in the $\delta^{13}C$ signatures of SOM and plant roots. However, due to methodological constraints, the results from this experiment were unreliable and further research is required.

Secondly, this study, along with other studies, has suggested that changes in plant community composition can change the proportion of recalcitrant and labile forms of C through its alteration in litter quality. This has direct effects on the microbial decomposition of SOM, as soil bacteria and fungi can

have differing capacities to degrade available and complex forms of plant derived C (Berg and Laskowski, 2005). In a recent study based on the same elevation gradient in Peru, the relative abundance of microbial functional groups were found to be an important determinant of Rh responses to changing C inputs (Whitaker et al., 2014). Therefore, in order to understand why changes in soil respiration might be occurring and what is driving these changes, any changes in the microbial communities need to be determined.

There is also a need for further exploration of the chemical structure of SOM. The density fractionation technique used in this study was useful for determining how the long and short term stores of C within the soil matrix had changed under different land uses and the application of natural abundance isotopes gave us an idea of the origin of C in the pasture soils. This can be taken further by performing ^{13}C nuclear magnetic resonance (NMR) spectroscopy and radiocarbon (^{14}C) modelling to get a better idea of the chemical structure of SOM by approximating the relative abundance of organic C functional groups, which can vary with decay and microbial processing (Baldock et al., 1992), and the turnover times of the decomposing SOM that contributes the most to soil respiration (Veldkamp, 1994). The combination of these techniques would provide a powerful assessment of the nature of soil C pools under different land uses.

Another aspect of soil C research which is gaining momentum is the importance of deeper soil layers for C storage. Evidence suggests that these deeper layers contain even greater soil C stocks than the surface soils and it is unclear how this deep soil is affected by land use changes (Rumpel and Kögel-Knabner, 2011). Most land use change study focus on the first 30 cm but certain land management techniques, deep roots and erosion can all have an effect on the subsurface layers.

5.8 Concluding remarks

This thesis addresses the implications of land use change on soil organic matter in one Andean elevational gradient and addresses the feasibility and problems associated with measuring and monitoring below-ground carbon stocks, which is an essential step to further our mechanistic understanding of the tropical C cycle. The Andes are singularly important and relevant to global climate and biodiversity, but equally a fragile environment threatened by human activity and climate change. There is pressing need to fully understand the effects of both of these processes, particularly their interaction, if effective management of this tropical region is to take place. The conclusions of this study advocate as priority the need for larger spatial and temporal replication of measurements and analyses of soil C stocks relative to land use change to assess whether the patterns observed here show consistency when viewed in the long-term across different sites and soil types. The findings from this thesis are intended to broaden discussion on the effects of land-use change and land management on soil C storage and stimulate action towards the development of a model of soil C cycling which incorporates the complexity and interaction between environmental parameters and managed tropical forest ecosystems.

References

ACHARD, F., BEUCHLE, R., MAYAUX, P., STIBIG, H.-J., BODART, C., BRINK, A., CARBONI, S., DESCLÉE, B., DONNAY, F., EVA, H. D., LUPI, A., RAŠI, R., SELIGER, R. & SIMONETTI, D. 2014. Determination of tropical deforestation rates and related carbon losses from 1990 to 2010. *Global Change Biology,* 20**,** 2540-2554.

ACHARD, F., EVA, H. D., MAYAUX, P., STIBIG, H.-J. & BELWARD, A. 2004. Improved estimates of net carbon emissions from land cover change in the tropics for the 1990s. *Global Biogeochemical Cycles,* 18**,** GB2008.

ADACHI, M., BEKKU, Y. S., RASHIDAH, W., OKUDA, T. & KOIZUMI, H. 2006. Differences in soil respiration between different tropical ecosystems. *Applied Soil Ecology,* 34**,** 258-265.

AIDE, T. M. & GRAU, H. R. 2004. Globalization, Migration, and Latin American Ecosystems. *Science,* 305**,** 1915-1916.

ANDERSSON, M., MICHELSEN, A., JENSEN, M. & KJØLLER, A. 2004. Tropical savannah woodland: effects of experimental fire on soil microorganisms and soil emissions of carbon dioxide. *Soil Biology and Biochemistry,* 36**,** 849-858.

ASBJORNSEN, H., VELÁZQUEZ-ROSAS, N., GARCÍA-SORIANO, R. & GALLARDO-HERNÁNDEZ, C. 2005. Deep ground fires cause massive above- and below-ground biomass losses in tropical montane cloud forests in Oaxaca, Mexico. *Journal of Tropical Ecology,* 21**,** 427-434.

ASBJORNSEN, H. & WICKEL, B. 2009. Changing fire regimes in tropical montane cloud forests: a global synthesis. *Tropical Fire Ecology.* Springer Berlin Heidelberg.

ASNER, G. P., KELLER, M., PEREIRA, J. R., ZWEEDE, J. C. & SILVA, J. N. M. 2004. Canopy damage and recovery after selective logging in amazonia: field and satalite studies *Ecological Applications,* 14**,** 280-298.

ASNER, G. P., POWELL, G. V., MASCARO, J., KNAPP, D. E., CLARK, J. K., JACOBSON, J., KENNEDY-BOWDOIN, T., BALAJI, A., PAEZ-ACOSTA, G. & VICTORIA, E. 2010. High-resolution forest carbon stocks and emissions in the Amazon. *Proceedings of the National Academy of Sciences,* 107**,** 16738-16742.

BAE, K., LEE, D., FAHEY, T., WOO, S., QUAYE, A. & LEE, Y.-K. 2013. Seasonal variation of soil respiration rates in a secondary forest and agroforestry systems. *Agroforestry Systems,* 87**,** 131-139.

BAISDEN, W. T., AMUNDSON, R., COOK, A. C. & BRENNER, D. L. 2002. Turnover and storage of C and N in five density fractions from California annual grassland surface soils. *Global Biogeochemical Cycles,* 16**,** 64-1-64-16.

BAJORIENĖ, K., JODAUGIENĖ, D., PUPALIENĖ, R. & SINKEVIČIENĖ, A. 2013. Effect of organic mulches on the content of organic carbon in the soil. *Estonian Journal of Ecology,* 62**,** 100œ106.

BALDOCK, J. A., OADES, J. M., WATERS, A. G., PENG, X., VASSALLO, A. M. & WILSON, M. A. 1992. Aspects of the Chemical Structure of Soil Organic Materials as Revealed by Solid-State ^{13}C NMR Spectroscopy. *Biogeochemistry,* 16**,** 1-42.

BALDOCK, J. A. & SKJEMSTAD, J. O. 2000. Role of the soil matrix and minerals in protecting natural organic materials against biological attack. *Organic Geochemistry,* 31**,** 697-710.

BALESDENT, J., WAGNER, G. & MARIOTTI, A. 1988. Soil organic matter turnover in long-term field experiments as revealed by carbon-13 natural abundance. *Soil Science Society of America Journal,* 52**,** 118-124.

BALSER, T. C. & WIXON, D. L. 2009. Investigating biological control over soil carbon temperature sensitivity. *Global Change Biology,* 15**,** 2935-2949.

BASHKIN, M. A. & BINKLEY, D. 1998. Changes in soil cabron following afforestation in Hawaii. *Ecology,* 79**,** 828-833.

BATES, D., MAECHLER, M., BOLKER, B., WALKER, S., CHRISTENSEN, R. H. B. & SINGMANN, H. 2014. Linear mixed-effects models using Eigen and S4.

BATJES, N. H. 1997. Possibilities for carbon sequestration in tropical and subtropical soils.

BAYER, C., MARTIN-NETO, L., MIELNICZUK, J., PILLON, C. N. & SANGOI, L. 2001. Changes in Soil Organic Matter Fractions under Subtropical No-Till Cropping Systems. *Soil Sci. Soc. Am. J.,* 65**,** 1473-1478.

BEKKU, Y. S., NAKATSUBO, T., KUME, A., ADACHI, M. & KOIZUMI, H. 2003. Effect of warming on the temperature dependence of soil respiration rate in arctic, temperate and tropical soils. *Applied Soil Ecology,* 22**,** 205-210.

BERG, B. & LASKOWSKI, R. 2005. Litter Decomposition: A Guide to Carbon and Nutrient Turnover. *In:* BJORN, B. & RYSZARD, L. (eds.) *Advances in Ecological Research.* Academic Press.

BERNER, R. A. & LASAGA, A. C. 1983. The carbonate-silicate geochemical cycle and its effect on atmospheric carbon dioxide over the past 100 million years. *Am. J. Sci,* 283**,** 641-683.

BLACK, G. & HARTGE, K. 1986. Bulk density. *Methods of soil analysis. Part,* 1**,** 347-380.

BOL, R., POIRIER, N., BALESDENT, J. & GLEIXNER, G. 2009. Molecular turnover time of soil organic matter in particle-size fractions of an arable soil. *Rapid Communications in Mass Spectrometry,* 23**,** 2551-2558.

BOSATTA, E. & ÅGREN, G. I. 1999. Soil organic matter quality interpreted thermodynamically. *Soil Biology and Biochemistry,* 31**,** 1889-1891.

BOUMA, T. & BRYLA, D. 2000. On the assessment of root and soil respiration for soils of different textures: interactions with soil moisture contents and soil CO_2 concentrations. *Plant and Soil,* 227**,** 215-221.

BOWDEN, R. D., NEWKIRK, K. M. & RULLO, G. M. 1998. Carbon dioxide and methane fluxes by a forest soil under laboratory-controlled moisture and temperature conditions. *Soil Biology and Biochemistry,* 30**,** 1591-1597.

BRADFORD, M. A., WATTS, B. W. & DAVIES, C. A. 2010. Thermal adaptation of heterotrophic soil respiration in laboratory microcosms. *Global Change Biology,* 16**,** 1576-1588.

BRADY, N. C. & WEIL, R. R. 1996. *The nature and properties of soils*, Prentice-Hall Inc.

BREMER, D. J., HAM, J. M., OWENSBY, C. E. & KNAPP, A. K. 1998. Responses of soil respiration to clipping and grazing in a tallgrass prairie. *Journal of Environmental Quality,* 27**,** 1539-1548.

BROOKS, T. M., MITTERMEIER, R. A., DA FONSECA, G. A. B., GERLACH, J., HOFFMANN, M., LAMOREUX, J. F., MITTERMEIER, C. G., PILGRIM, J. D. & RODRIGUES, A. S. L. 2006. Global Biodiversity Conservation Priorities. *Science,* 313**,** 58-61.

BROWN, S. 1982. The Storage and Production of Organic Matter in Tropical Forests and Their Role in the Global Carbon Cycle.

BUCKINGHAM, F. & SHANEE, S. 2009. Conservation priorities for the Peruvian yellow-tailed woolly monkey (Oreonax flavicauda): a GIS risk assessment and gap analysis. *Primate Conservation,* 24**,** 65-71.

BUTTERBACH-BAHL, K., KOCK, M., WILLIBALD, G., HEWETT, B., BUHAGIAR, S., PAPEN, H. & KIESE, R. 2004. Temporal variations of fluxes of NO, NO_2, N_2O, CO_2, and CH_4 in a tropical rain forest ecosystem. *Global Biogeochemical Cycles,* 18**,** GB3012.

CADISCH, G., IMHOF, H., URQUIAGA, S., BODDEY, R. M. & GILLER, K. E. 1996. Carbon turnover ($\delta^{13}C$) and nitrogen mineralization potential of particulate light soil organic matter after rainforest clearing. *Soil Biology and Biochemistry,* 28**,** 1555-1567.

CAMBARDELLA, C. & ELLIOTT, E. 1993. Carbon and nitrogen distribution in aggregates from cultivated and native grassland soils. *Soil Science Society of America Journal,* 57**,** 1071-1076.

CAMPBELL, G. S., JUNGBAUER, J. D. J., BRISTOW, K. L. & HUNGERFORD, R. D. 1995. Soil temperature and water content beneath a surface fire. *Soil Science,* 159**,** 363-374.

CAO, G., TANG, Y., MO, W., WANG, Y., LI, Y. & ZHAO, X. 2004. Grazing intensity alters soil respiration in an alpine meadow on the Tibetan plateau. *Soil Biology and Biochemistry,* 36**,** 237-243.

CARLYLE, J. C. & THAN, U. B. 1988. Abiotic Controls of Soil Respiration Beneath an Eighteen-Year-Old Pinus Radiata Stand in South-Eastern Australia. *Journal of Ecology,* 76**,** 654-662.

CERTINI, G. 2005. Effects of fire on properties of forest soils: a review. *Oecologia,* 143**,** 1-10.

CHAMBERS, J. Q., TRIBUZY, E. S., TOLEDO, L. C., CRISPIM, B. F., HIGUCHI, N., SANTOS, J. D., ARAÚJO, A. C., KRUIJT, B., NOBRE, A. D. & TRUMBORE, S. E. 2004. Respiraiton from tropical forest ecosystem: paritioning of sources and low carbon use effciciency. *Ecological Applications,* 14**,** 72-88.

CHAPIN III, F. S., MATSON, P. A. & VITOUSEK, P. 2011. *Principles of terrestrial ecosystem ecology,* Springer Science & Business Media.

CHEN, X., TANG, J., JIANG, L., LI, B., CHEN, J. & FANG, C. 2010. Evaluating the impacts of incubation procedures on estimated Q10 values of soil respiration. *Soil Biology and Biochemistry,* 42**,** 2282-2288.

CHEN, Y., LI, Y., AWADA, T., HAN, J. & LUO, Y. 2012. Carbon sequestration in the total and light fraction soil organic matter along a chronosequence in grazing exclosures in a semiarid degraded sandy site in China. *Journal of Arid Land,* 4**,** 411-419.

CHRISTENSEN, B. T. 2001. Physical fractionation of soil and structural and functional complexity in organic matter turnover. *European Journal of Soil Science,* 52**,** 345-353.

CLEEMPUT, O. V. & BOECKX, P. 2005. Alteración del ciclo del nitrógeno por las actividades agrícolas, sus consecuencias ambientales y sobre la salud humana. *Gayana. Botánica,* 62**,** 98-109.

CLEVELAND, C. C., WIEDER, W. R., REED, S. C. & TOWNSEND, A. R. 2010. Experimental drought in a tropical rain forest increases soil carbon dioxide losses to the atmosphere. *Ecology,* 91**,** 2313-2323.

COCHRANE, M. & RYAN, K. 2009. Fire and fire ecology: Concepts and principles. *Tropical Fire Ecology.* Springer Berlin Heidelberg.

COCHRANE, M. A. & BARBER, C. P. 2009. Climate change, human land use and future fires in the Amazon. *Global Change Biology,* 15**,** 601-612.

COLEMAN, K. & JENKINSON, D. 1996. RothC-26.3-A Model for the turnover of carbon in soil. *Evaluation of soil organic matter models.* Springer.

CONANT, R. T., RYAN, M. G., ÅGREN, G. I., BIRGE, H. E., DAVIDSON, E. A., ELIASSON, P. E., EVANS, S. E., FREY, S. D., GIARDINA, C. P., HOPKINS, F. M., HYVÖNEN, R., KIRSCHBAUM, M. U. F., LAVALLEE, J. M., LEIFELD, J., PARTON, W. J., MEGAN STEINWEG, J., WALLENSTEIN, M. D., MARTIN WETTERSTEDT, J. Å. & BRADFORD, M. A. 2011. Temperature and soil organic matter decomposition rates – synthesis of current knowledge and a way forward. *Global Change Biology,* 17**,** 3392-3404.

CRAINE, J. M. & GELDERMAN, T. M. 2011. Soil moisture controls on temperature sensitivity of soil organic carbon decomposition for a mesic grassland. *Soil Biology and Biochemistry,* 43**,** 455-457.

CURIEL YUSTE, J., BALDOCCHI, D. D., GERSHENSON, A., GOLDSTEIN, A., MISSON, L. & WONG, S. 2007. Microbial soil respiration and its dependency on carbon inputs, soil temperature and moisture. *Global Change Biology,* 13**,** 2018-2035.

DALIAS, P., ANDERSON, J., BOTTNER, P. & COÛTEAUX, M.-M. 2001. Long-term effects of temperature on carbon mineralisation processes. *Soil Biology and Biochemistry,* 33**,** 1049-1057.

DAVIDSON, E., VERCHOT, L., CATTÂNIO, J. H., ACKERMAN, I. & CARVALHO, J. E. M. 2000a. Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. *Biogeochemistry,* 48**,** 53-69.

DAVIDSON, E. A., ISHIDA, F. Y. & NEPSTAD, D. C. 2004. Effects of an experimental drought on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest. *Global Change Biology,* 10**,** 718-730.

DAVIDSON, E. A. & JANSSENS, I. A. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature,* 440**,** 165-73.

DAVIDSON, E. A., JANSSENS, I. A. & LUO, Y. 2006. On the variability of respiration in terrestrial ecosystems: moving beyond Q10. *Global Change Biology,* 12**,** 154-164.

DAVIDSON, E. A., TRUMBORE, S. E. & AMUNDSON, R. 2000b. Biogeochemistry: Soil warming and organic carbon content. *Nature,* 408**,** 789-790.

DAWSON, T. E., MAMBELLI, S., PLAMBOECK, A. H., TEMPLER, P. H. & TU, K. P. 2002. Stable Isotopes in Plant Ecology. *Annual Review of Ecology and Systematics,* 33**,** 507-559.

DELANEY, M., BROWN, S., LUGO, A. E., TORRES-LEZAMA, A. & QUINTERO, N. B. 1997. The distribution of organic carbon in major components of forests located in five life zones of Venezuela. *Journal of Tropical Ecology,* 13**,** 697-708.

DETWILER, R. P. 1986. Land use change and the global carbon cycle: the role of tropical soils. *Biogeochemistry,* 2**,** 67-93.

DIELEMAN, W. I. J., VENTER, M., RAMACHANDRA, A., KROCKENBERGER, A. K. & BIRD, M. I. 2013. Soil carbon stocks vary predictably with altitude in tropical forests: Implications for soil carbon storage. *Geoderma,* 204–205**,** 59-67.

DOFF SOTTA, E., MEIR, P., MALHI, Y., DONATO NOBRE, A., HODNETT, M. & GRACE, J. 2004. Soil CO2 efflux in a tropical forest in the central Amazon. *Global Change Biology,* 10**,** 601-617.

DON, A., SCHUMACHER, J. & FREIBAUER, A. 2011. Impact of tropical land-use change on soil organic carbon stocks - a meta-analysis. *Global Change Biology,* 17**,** 1658-1670.

EHLERINGER, J. R., BUCHMANN, N. & FLANAGAN, L. B. 2000. Carbon isotope ratios in belowground carbon cycle processes. *Ecological Applications,* 10**,** 412-422.

ELMORE, A. J. & ASNER, G. P. 2006. Effects of grazing intensity on soil carbon stocks following deforestation of a Hawaiian dry tropical forest. *Global Change Biology,* 12**,** 1761-1772.

EVA, H. D., BELWARD, A. S., DE MIRANDA, E. E., DI BELLA, C. M., GOND, V., HUBER, O., JONES, S., SGRENZAROLI, M. & FRITZ, S. 2004. A land cover map of South America. *Global Change Biology,* 10**,** 731-744.

FALKOWSKI, P., SCHOLES, R. J., BOYLE, E., CANADELL, J., CANFIELD, D., ELSER, J., GRUBER, N., HIBBARD, K., HÖGBERG, P., LINDER, S., MACKENZIE, F. T., MOORE III, B., PEDERSEN, T., ROSENTHAL, Y., SEITZINGER, S., SMETACEK, V. & STEFFEN, W. 2000. The Global Carbon Cycle: A Test of Our Knowledge of Earth as a System. *Science,* 290**,** 291-296.

FANG, C., SMITH, P., MONCRIEFF, J. B. & SMITH, J. U. 2005. Similar response of labile and resistant soil organic matter pools to changes in temperature. *Nature,* 433**,** 57-59.

FAO 2004. The state of food security in the world.

FAO. 2010. *Global Forest Resources Assessment 2010 Main Report*, FAO.

FEARNSIDE, P. 2000. Global Warming and Tropical Land-Use Change: Greenhouse Gas Emissions from Biomass Burning, Decomposition and Soils in Forest Conversion, Shifting Cultivation and Secondary Vegetation. *Climatic Change,* 46**,** 115-158.

FEARNSIDE, P. M. & IMBROZIO BARBOSA, R. 1998. Soil carbon changes from conversion of forest to pasture in Brazilian Amazonia. *Forest Ecology and Management,* 108**,** 147-166.

FEELEY, K. J. & SILMAN, M. R. 2010. Land-use and climate change effects on population size and extinction risk of Andean plants. *Global Change Biology,* 16**,** 3215-3222.

FELLER, C. & BEARE, M. H. 1997. Physical control of soil organic matter dynamics in the tropics. *Geoderma,* 79**,** 69-116.

FERNANDES, S. A. P., BERNOUX, M., CERRI, C. C., FEIGL, B. J. & PICCOLO, M. C. 2002. Seasonal variation of soil chemical properties and CO_2 and CH_4 fluxes in unfertilized and P-fertilized pastures in an Ultisol of the Brazilian Amazon. *Geoderma,* 107**,** 227-241.

FIERER, N., CRAINE, J. M., MCLAUCHLAN, K. & SCHIMEL, J. P. 2005. Litter quality and the temperature sensitivity of decompostion. *Ecology,* 86**,** 320-326.

FIGUEIREDO, C. C. D., RESCK, D. V. S. & CARNEIRO, M. A. C. 2010. Labile and stable fractions of soil organic matter under management systems and native cerrado. *Revista Brasileira de Ciência do Solo,* 34**,** 907-916.

FRANZLUEBBERS, A., STUEDEMANN, J., SCHOMBERG, H. & WILKINSON, S. 2000. Soil organic C and N pools under long-term pasture management in the Southern Piedmont USA. *Soil Biology and Biochemistry,* 32**,** 469-478.

FRANZLUEBBERS, A. J. 1999. Potential C and N mineralization and microbial biomass from intact and increasingly disturbed soils of varying texture. *Soil Biology and Biochemistry,* 31**,** 1083-1090.

FRANZLUEBBERS, A. J. & STUEDEMANN, J. A. 2002. Particulate and non-particulate fractions of soil organic carbon under pastures in the Southern Piedmont USA. *Environmental Pollution,* 116, Supplement 1**,** S53-S62.

FRIEDLINGSTEIN, P., MEINSHAUSEN, M., ARORA, V. K., JONES, C. D., ANAV, A., LIDDICOAT, S. K. & KNUTTI, R. 2013. Uncertainties in CMIP5 Climate Projections due to Carbon Cycle Feedbacks. *Journal of Climate,* 27**,** 511-526.

FU, G., ZHANG, X., YU, C., SHI, P., ZHOU, Y., LI, Y., YANG, P. & SHEN, Z. 2014. Response of soil respiration to grazing in an alpine meadow at three elevations in Tibet. *The Scientific World Journal,* 2014.

GABRIEL, C. E. & KELLMAN, L. 2011. Examining moisture and temperature sensitivity of soil organic matter decomposition in a temperate coniferous forest soil. *Biogeosciences Discuss.,* 8**,** 1369-1409.

GARCíA-OLIVA, F., SANFORD JR, R. L. & KELLY, E. 1999. Effects of slash-and-burn management on soil aggregate organic C and N in a tropical deciduous forest. *Geoderma,* 88**,** 1-12.

GENG, Y., WANG, Y., YANG, K., WANG, S., ZENG, H., BAUMANN, F., KUEHN, P., SCHOLTEN, T. & HE, J.-S. 2012. Soil Respiration in Tibetan Alpine Grasslands: Belowground Biomass and Soil Moisture, but Not Soil Temperature, Best Explain the Large-Scale Patterns. *PLoS ONE,* 7**,** e34968.

GEOEYE-1-SATELLITE 1984.

GHOLZ, H. L., WEDIN, D. A., SMITHERMAN, S. M., HARMON, M. E. & PARTON, W. J. 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Global Change Biology,* 6**,** 751-765.

GIBBON, A., SILMAN, M. R., MALHI, Y., FISHER, J. B., MEIR, P., ZIMMERMANN, M., DARGIE, G. C., FARFAN, W. R. & GARCIA, K. C. 2010. Ecosystem Carbon Storage Across the Grassland–Forest Transition in the High Andes of Manu National Park, Peru. *Ecosystems,* 13**,** 1097-1111.

GIRARDIN, C., ARAGÃO, L., MALHI, Y., HUARACA HUASCO, W., METCALFE, D., DURAND, L., MAMANI, M., SILVA-ESPEJO, J. & WHITTAKER, R. 2013. Fine root dynamics along an elevational gradient in tropical Amazonian and Andean forests. *Global Biogeochemical Cycles,* 27**,** 252-264.

GIRARDIN, C. A. J., MALHI, Y., ARAGÃO, L. E. O. C., MAMANI, M., HUARACA HUASCO, W., DURAND, L., FEELEY, K. J., RAPP, J., SILVA-ESPEJO, J. E., SILMAN, M., SALINAS, N. & WHITTAKER, R. J. 2010. Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology,* 16**,** 3176-3192.

GLASER, B., BALASHOV, E., HAUMAIER, L., GUGGENBERGER, G. & ZECH, W. 2000. Black carbon in density fractions of anthropogenic soils of the Brazilian Amazon region. *Organic Geochemistry,* 31**,** 669-678.

GOLCHIN, A., OADES, J., SKJEMSTAD, J. & CLARKE, P. 1994a. Soil structure and carbon cycling. *Soil Research,* 32**,** 1043-1068.

GOLCHIN, A., OADES, J., SKJEMSTAD, J. & CLARKE, P. 1994b. Study of free and occluded particulate organic matter in soils by solid state ^{13}C Cp/MAS NMR spectroscopy and scanning electron microscopy. *Soil Research,* 32**,** 285-309.

GOLDSTEIN, A. H., HULTMAN, N. E., FRACHEBOUD, J. M., BAUER, M. R., PANEK, J. A., XU, M., QI, Y., GUENTHER, A. B. & BAUGH, W. 2000. Effects of climate variability on the carbon dioxide, water, and sensible heat fluxes above a ponderosa pine plantation in the Sierra Nevada (CA). *Agricultural and Forest Meteorology,* 101**,** 113-129.

GONG, W., YAN, X.-Y., WANG, J.-Y., HU, T.-X. & GONG, Y.-B. 2009. Long-term manuring and fertilization effects on soil organic carbon pools under a wheat–maize cropping system in North China Plain. *Plant and Soil,* 314**,** 67-76.

GONZALEZ-PEREZ, J. A., GONZALEZ-VILA, F. J., ALMENDROS, G. & KNICKER, H. 2004. The effect of fire on soil organic matter - a review. *Environ Int,* 30**,** 855-70.

GRANT, R. F. & ROCHETTE, P. 1994. Soil Microbial Respiration at Different Water Potentials and Temperatures: Theory and Mathematical Modeling. *Soil Sci. Soc. Am. J.,* 58**,** 1681-1690.

GUGGENBERGER, G. & ZECH, W. 1999. Soil organic matter composition under primary forest, pasture, and secondary forest succession, Region Huetar Norte, Costa Rica. *Forest ecology and management,* 124**,** 93-104.

GUIMARÃES, D. V., GONZAGA, M. I. S., DA SILVA, T. O., DA SILVA, T. L., DA SILVA DIAS, N. & MATIAS, M. I. S. 2013. Soil organic matter pools and carbon fractions in soil under different land uses. *Soil and Tillage Research,* 126**,** 177-182.

GUO, L. B. & GIFFORD, R. M. 2002. Soil carbon stocks and land use change: a meta analysis. *Global Change Biology,* 8**,** 345-360.

HAGEDORN, F., MARTIN, M., RIXEN, C., RUSCH, S., BEBI, P., ZÜRCHER, A., SIEGWOLF, R. W., WIPF, S., ESCAPE, C., ROY, J. & HÄTTENSCHWILER, S. 2010. Short-term responses of ecosystem carbon fluxes to experimental soil warming at the Swiss alpine treeline. *Biogeochemistry,* 97**,** 7-19.

HAIRIAH, K., CADISCH, G., NOORDWIJK, M. V., LATIEF, A. R., MAHABHARATA, G. & SYEKHFANI, M. 1995. Size-density and isotopic fractionation of soil organic matter after forest conversion.

HALL, S., MCDOWELL, W. & SILVER, W. 2013. When Wet Gets Wetter: Decoupling of Moisture, Redox Biogeochemistry, and Greenhouse Gas Fluxes in a Humid Tropical Forest Soil. *Ecosystems,* 16**,** 576-589.

HARDEN, J. W., MARK, R. K., SUNDQUIST, E. T. & STALLARD, R. F. 1992. Dynamics of soil carbon during deglaciation of the Laurentide ice sheet. *Science,* 258**,** 1921-1924.

HARPER, C. W., BLAIR, J. M., FAY, P. A., KNAPP, A. K. & CARLISLE, J. D. 2005. Increased rainfall variability and reduced rainfall amount decreases soil CO_2 flux in a grassland ecosystem. *Global Change Biology,* 11**,** 322-334.

HARRIS, R. F. 1981. Effect of Water Potential on Microbial Growth and Activity. *In:* PARR, J. F., GARDNER, W. R. & ELLIOTT, L. F. (eds.) *Water Potential Relations in Soil Microbiology.* Soil Science Society of America.

HASHIMOTO, S., TANAKA, N., SUZUKI, M., INOUE, A., TAKIZAWA, H., KOSAKA, I., TANAKA, K., TANTASIRIN, C. & TANGTHAM, N. 2004. Soil respiration and soil CO_2 concentration in a tropical forest, Thailand. *Journal of Forest Research,* 9**,** 75-79.

HASSINK, J., WHITMORE, A. P. & KUBÁT, J. 1997. Size and density fractionation of soil organic matter and the physical capacity of soils to protect organic matter. *In:* ITTERSUM, M. K. V. & GEIJN, S. C. V. D. (eds.) *Developments in Crop Science.* Elsevier.

HELFRICH, M., LUDWIG, B., BUURMAN, P. & FLESSA, H. 2006. Effect of land use on the composition of soil organic matter in density and aggregate fractions as revealed by solid-state< sup> 13</sup> C NMR spectroscopy. *Geoderma,* 136**,** 331-341.

HIEDERER, R. & KÖCHY, M. 2011. *Global soil organic carbon estimates and the harmonized world soil database*, Citeseer.

HOFSTEDE, R. M. 1995. The effects of grazing and burning on soil and plant nutrient concentrations in Colombian páramo grasslands. *Plant and Soil,* 173**,** 111-132.

HOLLAND, E. A. & COLEMAN, D. C. 1987. Litter Placement Effects on Microbial and Organic Matter Dynamics in an Agroecosystem. *Ecology,* 68**,** 425-433.

HOLLAND, E. A., NEFF, J. C., TOWNSEND, A. R. & MCKEOWN, B. 2000. Uncertainties in the temperature sensitivity of decomposition in tropical and subtropical ecosystems: Implications for models. *Global Biogeochemical Cycles,* 14**,** 1137-1151.

HOLTGRIEVE, G. W., JEWETT, P. K. & MATSON, P. A. 2006. Variations in soil N cycling and trace gas emissions in wet tropical forests. *Oecologia,* 146**,** 584-594.

HOUGHTON, R. 2007. Balancing the global carbon budget. *Annu. Rev. Earth Planet. Sci.,* 35**,** 313-347.

HOUGHTON, R., HOBBIE, J., MELILLO, J. M., MOORE, B., PETERSON, B., SHAVER, G. & WOODWELL, G. 1983. Changes in the Carbon Content of Terrestrial Biota and Soils between 1860 and 1980: A Net Release of CO" 2 to the Atmosphere. *Ecological monographs,* 53**,** 235-262.

HOUGHTON, R., SKOLE, D., NOBRE, C. A., HACKLER, J., LAWRENCE, K. & CHOMENTOWSKI, W. H. 2000. Annual fluxes of carbon from deforestation and regrowth in the Brazilian Amazon. *Nature,* 403**,** 301-304.

HUFFMAN, E. L., MACDONALD, L. H. & STEDNICK, J. D. 2001. Strength and persistence of fire-induced soil hydrophobicity under ponderosa and lodgepole pine, Colorado Front Range. *Hydrological Processes,* 15**,** 2877-2892.

HUGHES, R. F., KAUFFMAN, J. B. & JARAMILLO, V. J. 1999. Biomass, Carbon, and Nutrient Dynamics of Secondary Forests in a Humid Tropical Region of México. *Ecology,* 80**,** 1892-1907.

IMESON, A. C., VERSTRATEN, J. M., VAN MULLIGEN, E. J. & SEVINK, J. 1992. The effects of fire and water repellency on infiltration and runoff under Mediterranean type forest. *CATENA,* 19**,** 345-361.

IPCC 2007. Climate change 2007: Summary for Policymakers, in Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, UK, p. 17.

IPCC 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. *[Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp, doi:10.1017/CBO9781107415324.*

IPCC 2014. Climate Change 2014: Mitigation of Climate Change. Contribution of Working Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. *[Edenhofer, O., R. Pichs-Madruga, Y. Sokona, E. Farahani, S. Kadner, K. Seyboth, A. Adler, I. Baum, S. Brunner, P. Eickemeier, B. Kriemann, J. Savolainen, S. Schlömer, C. von Stechow, T. Zwickel and J.C. Minx (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.*

ISE, T. & MOORCROFT, P. R. 2006. The global-scale temperature and moisture dependencies of soil organic carbon decomposition: an analysis using a mechanistic decomposition model. *Biogeochemistry,* 80**,** 217-231.

JASTROW, J. D., MILLER, R. M. & LUSSENHOP, J. 1998. Contributions of interacting biological mechanisms to soil aggregate stabilization in restored prairie. *Soil Biology and Biochemistry,* 30**,** 905-916.

JENKINSON, D. S., ADAMS, D. E. & WILD, A. 1991. Model estimates of CO_2 emissions from soil in response to global warming. *Nature,* 351**,** 304-306.

JOBBÁGY, E. G. & JACKSON, R. B. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation *Ecological Applications,* 10**,** 423-436.

JOHANSSON, M. U., FETENE, M., MALMER, A. & GRANSTRÖM, A. 2012. Tending for Cattle: Traditional Fire Management in Ethiopian Montane Heathlands. *Ecology and Society,* 17.

JOHNSON, L. C. & MATCHETT, J. R. 2001. Fire and grazing regulate belowground processes in tallgrass prairie. *Ecology,* 82**,** 3377-3389.

KIRSCHBAUM, M. U. 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. *Soil Biology and biochemistry,* 27**,** 753-760.

KISSINGER, G. & HEROLD, M. 2012. Drivers of Deforestation and Forest Degradation: A Synthesis Report for REDD+ Policymakers.

KITOH, A., KUSUNOKI, S. & NAKAEGAWA, T. 2011. Climate change projections over South America in the late 21st century with the 20 and 60 km mesh Meteorological Research Institute atmospheric general circulation model (MRI-AGCM). *Journal of Geophysical Research: Atmospheres,* 116**,** D06105.

KNICKER, H. 2007. How does fire affect the nature and stability of soil organic nitrogen and carbon? A review. *Biogeochemistry,* 85**,** 91-118.

KNOKE, T., CALVAS, B., AGUIRRE, N., ROMÁN-CUESTA, R. M., GÜNTER, S., STIMM, B., WEBER, M. & MOSANDL, R. 2009. Can tropical farmers reconcile subsistence needs with forest conservation? *Frontiers in Ecology and the Environment,* 7**,** 548-554.

KUTSCH, W. L., BAHN, M. & HEINEMEYER, A. 2009. *Soil carbon dynamics: an integrated methodology*, Cambridge University Press.

KUTSCH, W. L., BAHN, M., HEINEMEYER, A., KUTSCH, W. L., BAHN, M. & HEINEMEYER, A. 2001. Soil carbon relations: an overview. 1-15.

KUTSCH, W. L., MICHAEL BAHN, & HEINEMEYER, A. E. 2010. *Soil Carbon Dynamics*, Cambridge University Press.

KUZYAKOV, Y. 2006. Sources of CO_2 efflux from soil and review of partitioning methods. *Soil Biology and Biochemistry,* 38**,** 425-448.

LAL, R. 2004. Soil carbon sequestration impacts on global climate change and food security. *science,* 304**,** 1623-1627.

LAMBIN, E. F. & MEYFROIDT, P. 2011. Global land use change, economic globalization, and the looming land scarcity. *Proceedings of the National Academy of Sciences,* 108**,** 3465-3472.

LAURANCE, W. F. & WILLIAMSON, G. B. 2001. Positive Feedbacks among Forest Fragmentation, Drought, and Climate Change in the Amazon

Retroalimentaciones Positivas entre Fragmentación de Bosques, Sequía y Cambio Climático en el Amazonas. *Conservation Biology,* 15**,** 1529-1535.

LE QUERE, C., RAUPACH, M. R., CANADELL, J. G., MARLAND, G. & ET AL. 2009. Trends in the sources and sinks of carbon dioxide. *Nature Geosci,* 2**,** 831-836.

LEIFELD, J. & KÖGEL-KNABNER, I. 2005. Soil organic matter fractions as early indicators for carbon stock changes under different land-use? *Geoderma,* 124**,** 143-155.

LEMMA, B., KLEJA, D. B., NILSSON, I. & OLSSON, M. 2006. Soil carbon sequestration under different exotic tree species in the southwestern highlands of Ethiopia. *Geoderma,* 136**,** 886-898.

LI, C., FROLKING, S. & HARRISS, R. 1994. Modeling carbon biogeochemistry in agricultural soils. *Global biogeochemical cycles,* 8**,** 237-254.

LI, Y., DONG, S., WEN, L., WANG, X. & WU, Y. 2013. The effects of fencing on carbon stocks in the degraded alpine grasslands of the Qinghai-Tibetan Plateau. *Journal of Environmental Management,* 128**,** 393-399.

LI, Y., XU, M., ZOU, X., SHI, P. & ZHANG, Y. 2005. Comparing soil organic carbon dynamics in plantation and secondary forest in wet tropics in Puerto Rico. *Global Change Biology,* 11**,** 239-248.

LINN, D. & DORAN, J. 1984. Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and nontilled soils. *Soil Science Society of America Journal,* 48**,** 1267-1272.

LIVINGSTON, G. & HUTCHINSON, G. 1995. Enclosure-based measurement of trace gas exchange: applications and sources of error. *Biogenic trace gases: measuring emissions from soil and water***,** 14-51.

LLOYD, J., GRACE, J., MIRANDA, A. C., MEIR, P., WONG, S., MIRANDA, H. S., WRIGHT, I., GASH, J. & MCINTYRE, J. 1995. A simple calibrated model of Amazon rainforest productivity based on leaf biochemical properties. *Plant, Cell & Environment,* 18**,** 1129-1145.

LLOYD, J. & TAYLOR, J. 1994. On the temperature dependence of soil respiration. *Functional ecology***,** 315-323.

LUGO, A. E. & BROWN, S. 1992. Tropical forests as sinks of atmospheric carbon. *Forest Ecology and Management,* 54**,** 239-255.

LUO 2006. Yiqi Luo and Xuhui Zhou, Soil respiration and the environment. San Diego, CA : Elsevier, 2006.

LUO, Y. & ZHOU, X. 2006. Chapter 1 - Introduction and overview. *Soil Respiration and the Environment.* Burlington: Academic Press.

LUO, Y. & ZHOU, X. 2010. *Soil respiration and the environment,* Academic press.

LUTEYN, J. L. 1992. *Páramo: an Andean ecosystem under human influence*, Academic Press London (UK).

MALHI, Y. 2010. The carbon balance of tropical forest regions, 1990–2005. *Current Opinion in Environmental Sustainability,* 2**,** 237-244.

MALHI, Y. & GRACE, J. 2000. Tropical forests and atmospheric carbon dioxide. *Trends in Ecology & Evolution,* 15**,** 332-337.

MARÌN-SPIOTTA, E., CUSACK, D., OSTERTAG, R. & SILVER, W. 2008. Trends in Above and Belowground Carbon with Forest Regrowth After Agricultural Abandonment in the Neotropics. *Post-Agricultural Succession in the Neotropics.* Springer New York.

MARÍN-SPIOTTA, E. & SHARMA, S. 2013. Carbon storage in successional and plantation forest soils: a tropical analysis. *Global Ecology and Biogeography,* 22**,** 105-117.

MARIN-SPIOTTA, E., SILVER, W. L., SWANSTON, C. W. & OSTERTAG, R. 2009. Soil organic matter dynamics during 80 years of reforestation of tropical pastures. *Global Change Biology,* 15**,** 1584-1597.

MARÍN-SPIOTTA, E., SWANSTON, C. W., TORN, M. S., SILVER, W. L. & BURTON, S. D. 2008. Chemical and mineral control of soil carbon turnover in abandoned tropical pastures. *Geoderma,* 143**,** 49-62.

MCCULLEY, R. L., BOUTTON, T. W. & ARCHER, S. R. 2007. Soil respiration in a subtropical savanna parkland: Response to water additions. *Soil Science Society of America Journal,* 71**,** 820-828.

MCINTOSH, P. D., ALLEN, R. B. & SCOTT, N. 1997. Effects of Exclosure and Management on Biomass and Soil Nutrient Pools in Seasonally Dry High Country, New Zealand. *Journal of Environmental Management,* 51**,** 169-186.

MCLEAN, E. 1982. Soil pH and lime requirement. *Methods of soil analysis. Part 2. Chemical and microbiological properties***,** 199-224.

MCNABB, D. H. & SWANSON, F. J. 1990. Effects of fire on soil erosion. *Natural and prescribed fire in Pacific Northwest forests. J. Walstad, S. Radosevich, and D. Sandberg (editors). Oregon State University Press, Corvallis, Oreg***,** 159-176.

MCNABB, K., MILLER, M., LOCKABY, B., STOKES, B., CLAWSON, R., STANTURF, J. A. & SILVA, J. 1997. Selection harvests in Amazonian rainforests: long-term impacts on soil properties. *Forest Ecology and management,* 93**,** 153-160.

MEIR, P., GRACE, J., MIRANDA, A. & LLOYD, J. 1996. Soil respiration in a rainforest in Amazonia and in cerrado in central Brazil.

MELLING, L., GOH, K. J., CHADDY, A. & HATANO, R. 2014. Soil CO_2 Fluxes from Different Ages of Oil Palm in Tropical Peatland of Sarawak, Malaysia. *Soil Carbon.* Springer.

MELLING, L., HATANO, R. & GOH, K. J. 2005. Soil CO_2 flux from three ecosystems in tropical peatland of Sarawak, Malaysia. *Tellus B,* 57**,** 1-11.

METCALFE, D. B., MEIR, P., ARAGÃO, L. E. O. C., MALHI, Y., DA COSTA, A. C. L., BRAGA, A., GONÇALVES, P. H. L., DE ATHAYDES, J., DE ALMEIDA, S. S. & WILLIAMS, M. 2007. Factors controlling spatio-temporal variation in carbon dioxide efflux from surface litter, roots, and soil organic matter at four rain forest sites in the eastern Amazon. *Journal of Geophysical Research: Biogeosciences,* 112**,** G04001.

MICHELSEN, A., ANDERSSON, M., JENSEN, M., KJØLLER, A. & GASHEW, M. 2004. Carbon stocks, soil respiration and microbial biomass in fire-prone tropical grassland, woodland and forest ecosystems. *Soil Biology and Biochemistry,* 36**,** 1707-1717.

MO, J., ZHANG, W., ZHU, W., FANG, Y., LI, D. & ZHAO, P. 2007. Response of soil respiration to simulated N deposition in a disturbed and a rehabilitated tropical forest in southern China. *Plant and Soil,* 296**,** 125-135.

MORA, C., FRAZIER, A. G., LONGMAN, R. J., DACKS, R. S., WALTON, M. M., TONG, E. J., SANCHEZ, J. J., KAISER, L. R., STENDER, Y. O., ANDERSON, J. M., AMBROSINO, C. M., FERNANDEZ-SILVA, I., GIUSEFFI, L. M. & GIAMBELLUCA, T. W. 2013. The projected timing of climate departure from recent variability. *Nature,* 502**,** 183-187.

MOYANO, F. E., VASILYEVA, N., BOUCKAERT, L., COOK, F., CRAINE, J., CURIEL YUSTE, J., DON, A., EPRON, D., FORMANEK, P., FRANZLUEBBERS, A., ILSTEDT, U., KÄTTERER, T., ORCHARD, V., REICHSTEIN, M., REY, A., RUAMPS, L., SUBKE, J. A., THOMSEN, I. K. & CHENU, C. 2012. The moisture response of soil heterotrophic respiration: interaction with soil properties. *Biogeosciences,* 9**,** 1173-1182.

MUELLER, C. W. & KOEGEL-KNABNER, I. 2008. Soil organic carbon stocks, distribution, and composition affected by historic land use changes on adjacent sites. *Biology and Fertility of Soils,* 45**,** 347-359.

MUÑOZ, M. A., FAZ, A. & ZORNOZA, R. 2013. Carbon stocks and dynamics in grazing highlands from the Andean Plateau. *Catena,* 104**,** 136-143.

MURTY, D., KIRSCHBAUM, M. U. F., MCMURTRIE, R. E. & MCGILVRAY, H. 2002. Does conversion of forest to agricultural land change soil carbon and nitrogen? a review of the literature. *Global Change Biology,* 8**,** 105-123.

MUTUO, P., CADISCH, G., ALBRECHT, A., PALM, C. A. & VERCHOT, L. 2005. Potential of agroforestry for carbon sequestration and mitigation of greenhouse gas emissions from soils in the tropics. *Nutrient Cycling in Agroecosystems,* 71**,** 43-54.

NAHRAWI, H., HUSNI, M., OTHMAN, R. & BAH, A. 2011. Decomposition of leaf and fine root residues of three different crop species in tropical peat under controlled condition. *Malaysian Journal of Soil Science,* 15**,** 63-74.

NEARY, D. G., KLOPATEK, C. C., DEBANO, L. F. & FFOLLIOTT, P. F. 1999. Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management,* 122**,** 51-71.

NIINISTÖ, S., KELLOMÄKI, S., SILVOLA, J. & STOY, P. 2011. Seasonality in a boreal forest ecosystem affects the use of soil temperature and moisture as predictors of soil CO 2 efflux. *Biogeosciences,* 8.

NYE, P. H. & GREENLAND, D. J. 1964. Changes in the soil after clearing tropical forest. *Plant and Soil,* 21**,** 101-112.

OELBERMANN, M., ENGLISH, M. & SCHIFF, S. L. 2008. Evaluating carbon dynamics and microbial activity in arctic soils under warmer temperatures. *Canadian Journal of Soil Science,* 88**,** 31-44.

OJIMA, D. S., SCHIMEL, D., PARTON, W. & OWENSBY, C. 1994. Long-and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry,* 24**,** 67-84.

OLIVEIRA, P. J., ASNER, G. P., KNAPP, D. E., ALMEYDA, A., GALVÁN-GILDEMEISTER, R., KEENE, S., RAYBIN, R. F. & SMITH, R. C. 2007. Land-use allocation protects the Peruvian Amazon. *Science,* 317**,** 1233-1236.

OLIVERAS, I., GIRARDIN, C., DOUGHTY, C. E., CAHUANA, N., ARENAS, C. E., OLIVER, V., HUASCO, W. H. & MALHI, Y. 2014. Andean grasslands are as productive as tropical cloud forests. *Environmental Research Letters,* 9**,** 115011.

OLIVERAS, I., MALHI, Y., SALINAS, N., HUAMAN, V., URQUIAGA-FLORES, E., KALA-MAMANI, J., QUINTANO-LOAIZA, J. A., CUBA-TORRES, I., LIZARRAGA-MORALES, N. & ROMÁN-CUESTA, R.-M. 2013. Changes in forest structure and composition after fire in tropical montane cloud forests near the Andean treeline. *Plant Ecology & Diversity,* 7**,** 329-340.

ORCHARD, V. A. & COOK, F. J. 1983. Relationship between soil respiration and soil moisture. *Soil Biology and Biochemistry,* 15**,** 447-453.

OSMAN, K. T. 2012. *Soils: principles, properties and management*, Springer.

PAN, Y., BIRDSEY, R. A., FANG, J., HOUGHTON, R., KAUPPI, P. E., KURZ, W. A., PHILLIPS, O. L., SHVIDENKO, A., LEWIS, S. L. & CANADELL, J. G. 2011. A large and persistent carbon sink in the world's forests. *Science,* 333**,** 988-993.

PARTON, W. J., STEWART, J. W. B. & COLE, C. V. 1988. Dynamics of C, N, P and S in grassland soils: a model. *Biogeochemistry,* 5**,** 109-131.

PAUL, S., FLESSA, H., VELDKAMP, E. & LÓPEZ-ULLOA, M. 2008. Stabilization of recent soil carbon in the humid tropics following land use changes: evidence from aggregate fractionation and stable isotope analyses. *Biogeochemistry,* 87**,** 247-263.

PEDERSEN, A. R., PETERSEN, S. O. & SCHELDE, K. 2010. A comprehensive approach to soil-atmosphere trace-gas flux estimation with static chambers. *European Journal of Soil Science,* 61**,** 888-902.

PENDALL, E., SCHWENDENMANN, L., RAHN, T., MILLER, J. B., TANS, P. P. & WHITE, J. W. C. 2010. Land use and season affect fluxes of CO_2, CH_4, CO, N_2O, H_2 and isotopic source signatures in Panama: evidence from nocturnal boundary layer profiles. *Global Change Biology,* 16**,** 2721-2736.

PENMAN, J., GYTARSKY, M. & HIRAISHI, T. 2003. Intergovernmental Panel on Climate Change, National Greenhouse Gas Inventories Programme. Institute for Global Environmental Strategies, Kanagawa, Japan.

PICCOLO, G. A., GALANTINI, J. A. & ROSELL, R. A. 2004. Organic carbon fractions in a yerba mate plantation on a subtropical Kandihumult of Argentina. *Geoderma,* 123**,** 333-341.

PINTO, A. S., BUSTAMANTE, M. M. C., DA SILVA, M. R. S. S., KISSELLE, K. W., BROSSARD, M., KRUGER, R., ZEPP, R. G. & BURKE, R. A. 2006. Effects of Different Treatments of Pasture Restoration on Soil Trace Gas Emissions in the Cerrados of Central Brazil. *Earth Interactions,* 10**,** 1-26.

POEPLAU, C. & DON, A. 2013. Sensitivity of soil organic carbon stocks and fractions to different land-use changes across Europe. *Geoderma,* 192**,** 189-201.

POEPLAU, C., DON, A., VESTERDAL, L., LEIFELD, J., VAN WESEMAEL, B. A. S., SCHUMACHER, J. & GENSIOR, A. 2011. Temporal dynamics of soil organic carbon after land-use change in the temperate zone – carbon response functions as a model approach. *Global Change Biology,* 17**,** 2415-2427.

POST, W. M., EMANUEL, W. R., ZINKE, P. J. & STANGENBERGER, A. G. 1982. Soil carbon pools and world life zones. *Nature.*

POST, W. M. & KWON, K. C. 2000. Soil carbon sequestration and land-use change: processes and potential. *Global Change Biology,* 6**,** 317-327.

POST, W. M., PENG, T. H., EMANUEL, W. R., KING, A. W., DALE, V. H. & DEANGELIS, D. L. 1990. The global carbon cycle. *American Scientist,* 78**,** 310-326.

POWERS, J. S. 2004. Changes in Soil Carbon and Nitrogen after Contrasting Land-use Transitions in Northeastern Costa Rica. *Ecosystems,* 7.

POWLSON, D., BHOGAL, A., CHAMBERS, B., COLEMAN, K., MACDONALD, A., GOULDING, K. & WHITMORE, A. 2012. The potential to increase soil carbon stocks through reduced tillage or organic material additions in England and Wales: a case study. *Agriculture, Ecosystems & Environment,* 146**,** 23-33.

PRENTICE, I. C. 2001. The carbon cycle and atmospheric carbon dioxide.

QAYYUM, M., STEFFENS, D., REISENAUER, H. & SCHUBERT, S. 2014. Biochars influence differential distribution and chemical composition of soil organic matter.

R_CORE_TEAM 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing *Vienna, Austria. ISBN 3-900051-07-0, URL*.

RAICH, J. & SCHLESINGER, W. H. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus B,* 44**,** 81-99.

RAICH, J. W. 1998. Aboveground productivity and soil respiration in three Hawaiian rain forests. *Forest Ecology and Management,* 107**,** 309-318.

RAICH, J. W., POTTER, C. S. & BHAGAWATI, D. 2002. Interannual variability in global soil respiration, 1980–94. *Global Change Biology,* 8**,** 800-812.

RAICH, J. W. & TUFEKCIOGUL, A. 2000. Vegetation and soil respiration: correlations and controls. *Biogeochemistry,* 48**,** 71-90.

RAMANKUTTY, N., GIBBS, H. K., ACHARD, F., DEFRIES, R., FOLEY, J. A. & HOUGHTON, R. A. 2007. Challenges to estimating carbon emissions from tropical deforestation. *Global Change Biology,* 13**,** 51-66.

RAMSAY, P. M. 1992. *The páramo vegetation of Ecuador: the community ecology, dynamics and productivity of tropical grasslands in the Andes.*

RASSE, D., RUMPEL, C. & DIGNAC, M.-F. 2005. Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant and Soil,* 269**,** 341-356.

REEDER, J. D. & SCHUMAN, G. E. 2002. Influence of livestock grazing on C sequestration in semi-arid mixed-grass and short-grass rangelands. *Environmental Pollution,* 116**,** 457-463.

REICHSTEIN, M., KÄTTERER, T., ANDRÉN, O., CIAIS, P., SCHULZE, E.-D., CRAMER, W., PAPALE, D. & VALENTINI, R. 2005a. Temperature sensitivity of decomposition in relation to soil organic matter pools: critique and outlook. *Biogeosciences,* 2**,** 317-321.

REICHSTEIN, M., KÄTTERER, T., ANDRÉN, O., CIAIS, P., SCHULZE, E. D., CRAMER, W., PAPALE, D. & VALENTINI, R. 2005b. Temperature sensitivity of decomposition in relation to soil organic matter pools: critique and outlook. *Biogeosciences,* 2**,** 317-321.

REINERS, W. A., BOUWMAN, A. F., PARSONS, W. F. J. & KELLER, M. 1994. Tropical Rain Forest Conversion to Pasture: Changes in Vegetation and Soil Properties. *Ecological Applications,* 4**,** 363-377.

RHOADES, C. C., ECKERT, G. E. & COLEMAN, D. C. 2000. Soil carbon differences amoung forest, agriculture and secondary vegetation in lower montane Ecuador. *Ecological Applications,* 10**,** 497-505.

ROBERTSON, A. L., MALHI, Y., FARFAN-AMEZQUITA, F., ARAGÃO, L. E. O. C., SILVA ESPEJO, J. E. & ROBERTSON, M. A. 2010. Stem respiration in tropical forests along an elevation gradient in the Amazon and Andes. *Global Change Biology,* 16**,** 3193-3204.

RODRIGO, A., RECOUS, S., NEEL, C. & MARY, B. 1997. Modelling temperature and moisture effects on C–N transformations in soils: comparison of nine models. *Ecological Modelling,* 102**,** 325-339.

RODRIGUES, J. L., PELLIZARI, V. H., MUELLER, R., BAEK, K., JESUS EDA, C., PAULA, F. S., MIRZA, B., HAMAOUI, G. S., JR., TSAI, S. M., FEIGL, B., TIEDJE, J. M., BOHANNAN, B. J. &

NUSSLEIN, K. 2013. Conversion of the Amazon rainforest to agriculture results in biotic homogenization of soil bacterial communities. *Proc Natl Acad Sci U S A,* 110**,** 988-93.

ROLLINS, M. S., COHEN, A. D. & DURIG, J. R. 1993. Effects of fires on the chemical and petrographic composition of peat in the Snuggedy Swamp, South Carolina. *International Journal of Coal Geology,* 22**,** 101-117.

ROMÁN-CUESTA, R. M., SALINAS, N., ASBJORNSEN, H., OLIVERAS, I., HUAMAN, V., GUTIÉRREZ, Y., PUELLES, L., KALA, J., YABAR, D., ROJAS, M., ASTETE, R., JORDÁN, D. Y., SILMAN, M., MOSANDL, R., WEBER, M., STIMM, B., GÜNTER, S., KNOKE, T. & MALHI, Y. 2011. Implications of fires on carbon budgets in Andean cloud montane forest: The importance of peat soils and tree resprouting. *Forest Ecology and Management,* 261**,** 1987-1997.

RUKAZAMBUGA, N., GOLD, C., GOWEN, S. & RAGAMA, P. 2002. The influence of crop management on banana weevil, Cosmopolites sordidus (Coleoptera: Curculionidae) populations and yield of highland cooking banana (cv. Atwalira) in Uganda. *Bulletin of entomological research,* 92**,** 413-421.

RUMPEL, C. & KÖGEL-KNABNER, I. 2011. Deep soil organic matter—a key but poorly understood component of terrestrial C cycle. *Plant and Soil,* 338**,** 143-158.

RYAN, M. G. & LAW, B. E. 2005. Interpreting, measuring, and modeling soil respiration. *Biogeochemistry,* 73**,** 3-27.

SALA, O. E., CHAPIN, F. S., ARMESTO, J. J., BERLOW, E., BLOOMFIELD, J., DIRZO, R., HUBER-SANWALD, E., HUENNEKE, L. F., JACKSON, R. B. & KINZIG, A. 2000. Global biodiversity scenarios for the year 2100. *science,* 287**,** 1770-1774.

SALIMON, C., DAVIDSON, E., VICTORIA, R. & MELO, A. 2004. CO2 flux from soil in pastures and forests in southwestern Amazonia. *Global Change Biology,* 10**,** 833-843.

SALIMON, C. I. & DAVIDSON, E. A. 2008. Heterotrophic components of soil respiration in pastures and forests in southwestern Amazonia, Acre, Brazil. *Ambiente & Água-An Interdisciplinary Journal of Applied Science,* 3**,** 20-27.

SALINAS, N., MALHI, Y., MEIR, P., SILMAN, M., ROMAN CUESTA, R., HUAMAN, J., SALINAS, D., HUAMAN, V., GIBAJA, A., MAMANI, M. & FARFAN, F. 2011. The sensitivity of tropical leaf litter decomposition to temperature: results from a large-scale leaf translocation experiment along an elevation gradient in Peruvian forests. *New Phytol,* 189**,** 967-77.

SARMIENTO, F. O. 2002. Anthropogenic changes in the landscape of highland Ecuador. *Geographical Review,* 92**,** 213-234.

SCHARLEMANN, J. P., TANNER, E. V., HIEDERER, R. & KAPOS, V. 2014. Global soil carbon: understanding and managing the largest terrestrial carbon pool. *Carbon Management,* 5**,** 81-91.

SCHIMEL, D. S., BRASWELL, B. H., HOLLAND, E. A., MCKEOWN, R., OJIMA, D. S., PAINTER, T. H., PARTON, W. J. & TOWNSEND, A. R. 1994. Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. *Global Biogeochemical Cycles,* 8**,** 279-293.

SCHJØNNING, P., THOMSEN, I. K., MOLDRUP, P. & CHRISTENSEN, B. T. 2003. Linking soil microbial activity to water-and air-phase contents and diffusivities. *Soil Science Society of America Journal,* 67**,** 156-165.

SCHLESINGER, W. H. 1986. Changes in soil carbon storage and associated properties with disturbance and recovery. *The Changing Carbon Cycle.* Springer.

SCHMITT, A., PAUSCH, J. & KUZYAKOV, Y. 2013. Effect of clipping and shading on C allocation and fluxes in soil under ryegrass and alfalfa estimated by 14C labelling. *Applied Soil Ecology,* 64**,** 228-236.

SCHUUR, E. A., CHADWICK, O. A. & MATSON, P. A. 2001. Carbon cycling and soil carbon storage in mesic to wet Hawaiian montane forests. *Ecology,* 82**,** 3182-3196.

SCHWENDENMANN, L., PENDALL, E. & POTVIN, C. 2007. Surface soil organic carbon pools, mineralization and CO_2 efflux rates under different land-use types in Central Panama. *Stability of Tropical Rainforest Margins.* Springer.

SCHWENDENMANN, L., VELDKAMP, E., BRENES, T., O'BRIEN, J. & MACKENSEN, J. 2003. Spatial and temporal variation in soil CO_2 efflux in an old-growth neotropical rain forest, La Selva, Costa Rica. *Biogeochemistry,* 64**,** 111-128.

SILVER, W. L., LUGO, A. & KELLER, M. 1999. Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils. *Biogeochemistry,* 44**,** 301-328.

SILVER, W. L., NEFF, J., MCGRODDY, M., VELDKAMP, E., KELLER, M. & COSME, R. 2000. Effects of Soil Texture on Belowground Carbon and Nutrient Storage in a Lowland Amazonian Forest Ecosystem. *Ecosystems,* 3**,** 193-209.

SILVER, W. L., THOMPSON, A. W., MCGRODDY, M. E., VARNER, R. K., DIAS, J. D., SILVA, H., CRILL, P. M. & KELLER, M. 2005. Fine root dynamics and trace gas fluxes in two lowland tropical forest soils. *Global Change Biology,* 11**,** 290-306.

SIX, J., BOSSUYT, H., DEGRYZE, S. & DENEF, K. 2004. A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. *Soil and Tillage Research,* 79**,** 7-31.

SIX, J., CALLEWAERT, P., LENDERS, S., DE GRYZE, S., MORRIS, S. J., GREGORICH, E. G., PAUL, E. A. & PAUSTIAN, K. 2002a. Measuring and Understanding Carbon Storage in Afforested Soils by Physical Fractionation. *Soil Sci. Soc. Am. J.,* 66**,** 1981-1987.

SIX, J., CONANT, R., PAUL, E. & PAUSTIAN, K. 2002b. Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. *Plant and soil,* 241**,** 155-176.

SIX, J. & JASTROW, J. D. 2002. Organic matter turnover. *Encyclopedia of soil science. Marcel Dekker, New York,* 936-942.

SJÖGERSTEN, S. & WOOKEY, P. A. 2002. Climatic and resource quality controls on soil respiration across a forest–tundra ecotone in Swedish Lapland. *Soil Biology and Biochemistry,* 34**,** 1633-1646.

SKOPP, J., JAWSON, M. & DORAN, J. 1990. Steady-state aerobic microbial activity as a function of soil water content. *Soil Science Society of America Journal,* 54**,** 1619-1625.

SOLLINS, P., SWANSTON, C., KLEBER, M., FILLEY, T., KRAMER, M., CROW, S., CALDWELL, B. A., LAJTHA, K. & BOWDEN, R. 2006. Organic C and N stabilization in a forest soil: Evidence from sequential density fractionation. *Soil Biology and Biochemistry,* 38**,** 3313-3324.

SOON, Y. K., ARSHAD, M. A., HAQ, A. & LUPWAYI, N. 2007. The influence of 12 years of tillage and crop rotation on total and labile organic carbon in a sandy loam soil. *Soil and Tillage Research,* 95**,** 38-46.

SOTTA, E. D., VELDKAMP, E., SCHWENDENMANN, L., GUIMARAES, B. R., PAIXAO, R. K., RUIVO, M. D. L. P., DA COSTA, A. C. L., MEIR, P., SOTTA, E. D., VELDKAMP, E., SCHWENDENMANN, L., GUIMARAES, B. R., PAIXAO, R. K., RUIVO, M. D. L. P., DA COSTA, A.

C. L. & MEIR, P. 2007. Effects of an induced drought on soil carbon dioxide (CO_2) efflux and soil CO_2 production in an Eastern Amazonian rainforest, Brazil. *Global Change Biology,* 13**,** 2218-2229.

STARK, J. M. & FIRESTONE, M. K. 1995. Mechanisms for soil moisture effects on activity of nitrifying bacteria. *Applied and Environmental Microbiology,* 61**,** 218-221.

STEFFEN, W., NOBLE, I., CANADELL, J., APPS, M., SCHULZE, E.-D. & JARVIS, P. G. 1998. The terrestrial carbon cycle: implications for the Kyoto Protocol. *Science,* 280**,** 1393-1394.

STEFFENS, M., KÖLBL, A., TOTSCHE, K. U. & KÖGEL-KNABNER, I. 2008. Grazing effects on soil chemical and physical properties in a semiarid steppe of Inner Mongolia (P.R. China). *Geoderma,* 143**,** 63-72.

SU, Y.-Z., ZHAO, H.-L., ZHANG, T.-H. & ZHAO, X.-Y. 2004. Soil properties following cultivation and non-grazing of a semi-arid sandy grassland in northern China. *Soil and Tillage Research,* 75**,** 27-36.

SUSEELA, V., CONANT, R. T., WALLENSTEIN, M. D. & DUKES, J. S. 2012. Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. *Global Change Biology,* 18**,** 336-348.

TAN, Z., LAL, R., OWENS, L. & IZAURRALDE, R. 2007. Distribution of light and heavy fractions of soil organic carbon as related to land use and tillage practice. *Soil and Tillage Research,* 92**,** 53-59.

TANS, P. & KEELING, R. 2014. NOAA/ESRL (www.esrl.noaa.gov/gmd/ccgg/trends/), Scripps Institution of Oceanography (scrippsco2.ucsd.edu/).

TEH, Y. A., DIEM, T., JONES, S., HUARACA QUISPE, L. P., BAGGS, E., MORLEY, N., RICHARDS, M., SMITH, P. & MEIR, P. 2014. Methane and nitrous oxide fluxes across an elevation gradient in the tropical Peruvian Andes. *Biogeosciences,* 11**,** 2325-2339.

TELLES, E. D. C. C., DE CAMARGO, P. B., MARTINELLI, L. A., TRUMBORE, S. E., DA COSTA, E. S., SANTOS, J., HIGUCHI, N. & OLIVEIRA, R. C. 2003. Influence of soil texture on carbon dynamics and storage potential in tropical forest soils of Amazonia. *Global Biogeochemical Cycles,* 17**,** n/a-n/a.

THOMSEN, I. K., SCHJØNNING, P., JENSEN, B., KRISTENSEN, K. & CHRISTENSEN, B. T. 1999. Turnover of organic matter in differently textured soils: II. Microbial activity as influenced by soil water regimes. *Geoderma,* 89**,** 199-218.

TIESSEN, H. & STEWART, J. 1983. Particle-size fractions and their use in studies of soil organic matter: II. Cultivation effects on organic matter composition in size fractions. *Soil Science Society of America Journal,* 47**,** 509-514.

TORN, M. S., TRUMBORE, S. E., CHADWICK, O. A., VITOUSEK, P. M. & HENDRICKS, D. M. 1997. Mineral control of soil organic carbon storage and turnover. *Nature,* 389**,** 170-173.

TOWNSEND, A. R., VITOUSEK, P. M. & TRUMBORE, S. E. 1995. Soil Organic Matter Dynamics Along Gradients in Temperature and Land Use on the Island of Hawaii. *Ecology,* 76**,** 721-733.

TRUMBORE, S. 2006. Carbon respired by terrestrial ecosystems – recent progress and challenges. *Global Change Biology,* 12**,** 141-153.

TRUMBORE, S., DA COSTA, E. S., NEPSTAD, D. C., BARBOSA DE CAMARGO, P., MARTINELLI, L. A., RAY, D., RESTOM, T. & SILVER, W. 2006. Dynamics of fine root carbon in Amazonian tropical ecosystems and the contribution of roots to soil respiration. *Global Change Biology,* 12**,** 217-229.

TRUMBORE, S. E. 1993. Comparison of carbon dynamics in tropical and temperate soils using radiocarbon measurements. *Global Biogeochemical Cycles,* 7**,** 275-290.

TRUMBORE, S. E., DAVIDSON, E. A., BARBOSA DE CAMARGO, P., NEPSTAD, D. C. & MARTINELLI, L. A. 1995. Belowground cycling of carbon in forests and pastures of eastern Amazonia. *Global Biogeochemical Cycles,* 9**,** 515-528.

UNEP 2011. United Nations Environment Programme (UNEP).

UNFCCC 1994. The United Nations Framework Convention on Climate Change.

URRUTIA, R. & VUILLE, M. 2009. Climate change projections for the tropical Andes using a regional climate model: Temperature and precipitation simulations for the end of the 21st century. *Journal of Geophysical Research,* 114.

VALDIVIA, G. 2014. Anthony Bebbington and Jeffrey Bury (eds): Subterranean Struggles: New Dynamics of Mining, Oil, and Gas in Latin America. *Human Ecology***,** 1-2.

VAN REENEN, C. A., VISSER, G. J. & LOOS, M. A. 1992. Soil Microorganisms and Activities in Relation to Season, Soil Factors and Fire. *In:* VAN WILGEN, B., RICHARDSON, D., KRUGER, F. & VAN HENSBERGEN, H. (eds.) *Fire in South African Mountain Fynbos.* Springer Berlin Heidelberg.

VAN WESEMAEL, B., PAUSTIAN, K., MEERSMANS, J., GOIDTS, E., BARANCIKOVA, G. & EASTER, M. 2010. Agricultural management explains historic changes in regional soil carbon stocks. *Proceedings of the National Academy of Sciences,* 107**,** 14926-14930.

VASCONCELOS, S. S., ZARIN, D. J., CAPANU, M., LITTELL, R., DAVIDSON, E. A., ISHIDA, F. Y., SANTOS, E. B., ARAÚJO, M. M., ARAGÃO, D. V., RANGEL-VASCONCELOS, L. G. T., DE ASSIS OLIVEIRA, F., MCDOWELL, W. H. & DE CARVALHO, C. J. R. 2004. Moisture and substrate availability constrain soil trace gas fluxes in an eastern Amazonian regrowth forest. *Global Biogeochemical Cycles,* 18**,** GB2009.

VELDKAMP, E. 1994. Organic Carbon Turnover in Three Tropical Soils under Pasture after Deforestation. *Soil Sci. Soc. Am. J.,* 58**,** 175-180.

VERA, C., SILVESTRI, G., LIEBMANN, B. & GONZÁLEZ, P. 2006. Climate change scenarios for seasonal precipitation in South America from IPCC-AR4 models. *Geophysical research letters,* 33.

VICCA, S., BAHN, M., ESTIARTE, M., VAN LOON, E. E., VARGAS, R., ALBERTI, G., AMBUS, P., ARAIN, M. A., BEIER, C., BENTLEY, L. P., BORKEN, W., BUCHMANN, N., COLLINS, S. L., DE DATO, G., DUKES, J. S., ESCOLAR, C., FAY, P., GUIDOLOTTI, G., HANSON, P. J., KAHMEN, A., KRÖEL-DULAY, G., LADREITER-KNAUSS, T., LARSEN, K. S., LELLEI-KOVACS, E., LEBRIJA-TREJOS, E., MAESTRE, F. T., MARHAN, S., MARSHALL, M., MEIR, P., MIAO, Y., MUHR, J., NIKLAUS, P. A., OGAYA, R., PEÑUELAS, J., POLL, C., RUSTAD, L. E., SAVAGE, K., SCHINDLBACHER, A., SCHMIDT, I. K., SMITH, A. R., SOTTA, E. D., SUSEELA, V., TIETEMA, A., VAN GESTEL, N., VAN STRAATEN, O., WAN, S., WEBER, U. & JANSSENS, I. A. 2014. Can current moisture responses predict soil CO_2 efflux under altered precipitation regimes? A synthesis of manipulation experiments. *Biogeosciences Discuss.,* 11**,** 853-899.

VICTORIA, R., BANWART, S., BLACK, H., INGRAM, J., JOOSTEN, H. & MILNE, E. 2012. The benefits of soil carbon: UNEP Year Book.

VITOUSEK, P. M. 1984. Litterfall, Nutrient Cycling, and Nutrient Limitation in Tropical Forests. *Ecology,* 65**,** 285-298.

VON LÜTZOW, M. & KÖGEL-KNABNER, I. 2009. Temperature sensitivity of soil organic matter decomposition—what do we know? *Biology and Fertility of Soils,* 46**,** 1-15.

VUILLE, M., BRADLEY, R., WERNER, M. & KEIMIG, F. 2003. 20th Century Climate Change in the Tropical Andes: Observations and Model Results. *In:* DIAZ, H. (ed.) *Climate Variability and Change in High Elevation Regions: Past, Present & Future.* Springer Netherlands.

WALLENSTEIN, M., ALLISON, S. D., ERNAKOVICH, J., STEINWEG, J. M. & SINSABAUGH, R. 2011. Controls on the temperature sensitivity of soil enzymes: a key driver of in situ enzyme activity rates. *Soil enzymology.* Springer.

WANG, Q. & WANG, S. 2011. Response of labile soil organic matter to changes in forest vegetation in subtropical regions. *Applied Soil Ecology,* 47**,** 210-216.

WANG, W. & FANG, J. 2009. Soil respiration and human effects on global grasslands. *Global and Planetary Change,* 67**,** 20-28.

WARD, S., BARDGETT, R., MCNAMARA, N., ADAMSON, J. & OSTLE, N. 2007. Long-Term Consequences of Grazing and Burning on Northern Peatland Carbon Dynamics. *Ecosystems,* 10**,** 1069-1083.

WATSON, R. T., NOBLE, I. R., BOLIN, B., RAVINDRANATH, N. H., VERARDO, D. J. & DOKKEN, D. J. 2000. Land use, land-use change and forestry: a special report of the Intergovernmental Panel on Climate Change.

WEI, X., SHAO, M., GALE, W. & LI, L. 2014. Global pattern of soil carbon losses due to the conversion of forests to agricultural land. *Sci. Rep.,* 4.

WERF, G. V. D., MORTON, D., DEFRIES, R., GIGLIO, L., RANDERSON, J., COLLATZ, G. & KASIBHATLA, P. 2009. Estimates of fire emissions from an active deforestation region in the southern Amazon based on satellite data and biogeochemical modelling. *Biogeosciences,* 6**,** 235-249.

WERNER, C., ZHENG, X., TANG, J., XIE, B., LIU, C., KIESE, R. & BUTTERBACH-BAHL, K. 2006. N_2O, CH_4 and CO_2 emissions from seasonal tropical rainforests and a rubber plantation in Southwest China. *Plant and Soil,* 289**,** 335-353.

WETTERSTEDT, J. Å. M., PERSSON, T. & ÅGREN, G. I. 2010. Temperature sensitivity and substrate quality in soil organic matter decomposition: results of an incubation study with three substrates. *Global Change Biology,* 16**,** 1806-1819.

WHITAKER, J., OSTLE, N., NOTTINGHAM, A. T., CCAHUANA, A., SALINAS, N., BARDGETT, R. D., MEIR, P. & MCNAMARA, N. P. 2014. Microbial community composition explains soil respiration responses to changing carbon inputs along an Andes-to-Amazon elevation gradient. *Journal of Ecology,* 102**,** 1058-1071.

WICK, B. & TIESSEN, H. 2008. Organic Matter Turnover in Light Fraction and Whole Soil under Silvopastoral Land Use in Semiarid Northeast Brazil. *Rangeland Ecology & Management,* 61**,** 275-283.

WICKHAM, H. 2009. ggplot2: elegant graphics for data analysis. *Springer New York.*

WIEDER, W. R., CLEVELAND, C. C. & TOWNSEND, A. R. 2009. Controls over leaf litter decomposition in wet tropical forests. *Ecology,* 90**,** 3333-3341.

WOOD, T. E., CAVALERI, M. A. & REED, S. C. 2012. Tropical forest carbon balance in a warmer world: a critical review spanning microbial- to ecosystem-scale processes. *Biological Reviews,* 87**,** 912-927.

WOOD, T. E., DETTO, M. & SILVER, W. L. 2013. Sensitivity of Soil Respiration to Variability in Soil Moisture and Temperature in a Humid Tropical Forest. *PloS one,* 8**,** e80965.

WOOD, T. E. & SILVER, W. L. 2012. Strong spatial variability in trace gasdynamics following experimental drought in a humid tropical forest. *Global Biogeochemical Cycles,* 26**,** n/a-n/a.

WRIGHT, S. J. 2005. Tropical forests in a changing environment. *Trends in Ecology & Evolution,* 20**,** 553-560.

ZACKRISSON, O., NILSSON, M.-C. & WARDLE, D. A. 1996. Key ecological function of charcoal from wildfire in the Boreal forest. *Oikos***,** 10-19.

ZHOU, W., HUI, D. & SHEN, W. 2014. Effects of Soil Moisture on the Temperature Sensitivity of Soil Heterotrophic Respiration: A Laboratory Incubation Study. *PloS one,* 9**,** e92531.

ZIMMERMANN, M. & BIRD, M. I. 2012. Temperature sensitivity of tropical forest soil respiration increase along an altitudinal gradient with ongoing decomposition. *Geoderma,* 187–188**,** 8-15.

ZIMMERMANN, M., LEIFELD, J., CONEN, F., BIRD, M. I. & MEIR, P. 2010a. Can composition and physical protection of soil organic matter explain soil respiration temperature sensitivity? *Biogeochemistry,* 107**,** 423-436.

ZIMMERMANN, M., LEIFELD, J., SCHMIDT, M. W. I., SMITH, P. & FUHRER, J. 2007. Measured soil organic matter fractions can be related to pools in the RothC model. *European Journal of Soil Science,* 58**,** 658-667.

ZIMMERMANN, M., MEIR, P., BIRD, M., MALHI, Y. & CCAHUANA, A. 2009a. Litter contribution to diurnal and annual soil respiration in a tropical montane cloud forest. *Soil Biology and Biochemistry,* 41**,** 1338-1340.

ZIMMERMANN, M., MEIR, P., BIRD, M. I., MALHI, Y. & CCAHUANA, A. J. Q. 2009b. Climate dependence of heterotrophic soil respiration from a soil-translocation experiment along a 3000 m tropical forest altitudinal gradient. *European Journal of Soil Science,* 60**,** 895-906.

ZIMMERMANN, M., MEIR, P., BIRD, M. I., MALHI, Y. & CCAHUANA, A. J. Q. 2010b. Temporal variation and climate dependence of soil respiration and its components along a 3000 m altitudinal tropical forest gradient. *Global Biogeochemical Cycles,* 24**,** GB4012.

ZIMMERMANN, M., MEIR, P., SILMAN, M. R., FEDDERS, A., GIBBON, A., MALHI, Y., URREGO, D. H., BUSH, M. B., FEELEY, K. J., GARCIA, K. C., DARGIE, G. C., FARFAN, W. R., GOETZ, B. P., JOHNSON, W. T., KLINE, K. M., MODI, A. T., RURAU, N. M. Q., STAUDT, B. T. & ZAMORA, F. 2009c. No Differences in Soil Carbon Stocks Across the Tree Line in the Peruvian Andes. *Ecosystems,* 13**,** 62-74.

ZOGG, G. P., ZAK, D. R., RINGELBERG, D. B., WHITE, D. C., MACDONALD, N. W. & PREGITZER, K. S. 1997. Compositional and Functional Shifts in Microbial Communities Due to Soil Warming. *Soil Sci. Soc. Am. J.,* 61**,** 475-481.

ZUUR, A., IENO, E. N., WALKER, N., SAVELIEV, A. A. & SMITH, G. M. 2009. *Mixed effects models and extensions in ecology with R,* Springer Science & Business Media.

~ Appendices ~

1.1 Appendix for chapter 2

Table 1.1 Vegetation at the premontane elevation

Mature forest	**1.** Iriartea deltoidea (la mayoría son individuos muy jóvenes) **2.** Socratea exorrhiza (común) **3.** Socratea salazari (frecuente) **4.** Wetinia augusta (frecuente) **5.** Oenocarpus batawa (rara) **6.** Oenocarpus mapora (rara) **7.** Euterpe edulis (rara, aunque se encuentran juveniles) **8.** Geonoma cf. interrupta (frecuente, llamada comúnmente "cuyuli" es usada en la zona para techar, dura aproximadamente cuatro años, la mitad que G. deversa). **9.** Geonoma cf. acaulis (frecuente) **10.** Chamaedorea pinnatifrons (rara) **11.** Chamaedorea pauciflora (rara) **12.** Bactris simplicifrons (frecuente) **13.** Bactris macana o máxima (rara) **14.** Bactris maraja (rara) **15.** Astrocaryum murumuru (común)
Selective logging	Visibly affected by selective logging due to the absence of trees and shortages of pona (Iriartea deltoid), which is used extensively in construction and Wasai (Euterpe precatoria), which is used for extraction of palm; usually with plenty of paca (Guadua sp.); with understory dominated by shrubs, ferns, terrestrial aroids (Anthurium, Dieffenbachia) Cyclanthaceae (Cyclantus, Carludovica, Asplundia), Heliconia (4 species) and other herbaceous plants; at least 7 species of tree ferns.
Secondary forest	Forest thinning and strongly depleted in tree species; relatively continuous and of medium height (20 m) canopy; dominated by dense shrubby dicotyledonous middle sequence (Rubiaceae, Theophrastaceae) and presence of Heliconia (3 species, 2 are different from the forest hills), Carludovica palmata, understory palms (Geonoma acaulis, Chamaedorea pinnatifrons) understory and juvenile palms (Euterpe precatoria, Astrocaryum murumuru, Socratea exorrhiza); lianas and hemiepiphytes (Araceae) represented in abundance. Dominant tree species: **1.** Triplaris sp. (extremely common) **2.** Cecropia spp. (common) **3.** Ficus insipida 3 (common) **4.** Erythrina sp. (common) **5.** Sheflera morototoni (common) **6.** Pouruma cecropifolia (common) **7.** Mishikallo or filbert (Fabaceae, latin name?) **8.** Socratea exorrhiza (common) **9.** Astrocaryum murumuru
Abandoned pasture	4 shrubby vegetation with scattered trees Low vegetation (<5 m) shrub of piperaceae families melastomataceae, tall grasses (reeds, etc.); tree species of the same species in secondary forests contradas.

Table 1.2 Mean mass recovery (%) and contribution to bulk C (%) in density soil C fractions in burnt and grazed montane grasslands for each depth (0-5, 5-10, 10-20, 20-30 cm).

Fraction		Land use	0-5 cm	5-10 cm	10-20 cm	20-30 cm
LF	Fraction of total C (%)	G - B	29.3 ± 4.4^{b}	12.2 ± 4.8^{a}	6.1 ± 2.5^{b}	8.3 ± 2.6^{ab}
		G - NB	59.8 ± 6.3^{a}	24.4 ± 5.8^{a}	3.9 ± 0.2^{b}	2.8 ± 1.0^{b}
		NG - B	43.4 ± 6.2^{ab}	18.1 ± 5.1^{a}	11.1 ± 5.4^{ab}	6.2 ± 0.7^{ab}
		NG - NB	46.7 ± 5.4^{ab}	27.0 ± 3.3^{a}	20.4 ± 3.1^{a}	26.1 ± 7.3^{a}
	Mass of soil recovered (%)	G - B	19.3 ± 2.9^{b}	11.3 ± 2.6^{a}	6.17 ± 2.1^{ab}	2.7 ± 1.7^{b}
		G - NB	36.9 ± 3.6^{a}	23.1 ± 0.5^{a}	3.2 ± 0.9^{b}	1.6 ± 0.4^{b}
		NG - B	39.7 ± 4.9^{a}	13.1 ± 2.9^{a}	6.1 ± 2.7^{ab}	1.7 ± 0.6^{b}
		NG - NB	35.4 ± 1.1^{a}	18.9 ± 1.7^{a}	12.7 ± 2.5^{a}	11.1 ± 2.2^{a}
OLF	Fraction of total C (%)	G - B	18.0 ±4.2^{a}	8.4 ± 2.1^{a}	10.3 ± 4.2^{a}	6.2 ± 2.1^{a}
		G - NB	12.7± 2.6^{ab}	2.8 ± 0.9^{a}	10.0 ± 2.3^{a}	10.1 ± 4.0^{a}
		NG - B	21.6 ± 2.6^{a}	9.9 ± 2.8^{a}	12.3 ± 3.2^{a}	13.1 ± 2.5^{a}
		NG - NB	5.9 ± 1.2^{b}	7.2 ± 1.8^{a}	4.5 ± 0.9^{a}	3.4 ± 0.9^{a}
	Mass of soil recovered (%)	G - B	18.2 ± 2.0^{ab}	10.2 ± 2.2^{a}	9.1 ± 2.7^{a}	1.7 ± 0.5^{a}
		G - NB	10.1 ± 2.0^{bc}	3.5 ± 0.8^{a}	3.3 ± 0.4^{a}	4.5 ± 1.9^{a}
		NG - B	23.8 ± 4.0^{a}	10.5 ± 3.6^{a}	9.6 ± 1.4^{a}	1.2 ± 0.4^{a}
		NG - NB	5.0 ± 0.9^{c}	5.7 ± 1.1^{a}	4.2 ± 1.2^{a}	2.3 ± 0.9^{a}
HF	Fraction of total C (%)	G - B	52.3 ± 7.0^{a}	79.3 ± 5.1^{a}	86.5 ± 6.8^{a}	85.5 ± 4.4^{a}
		G - NB	27.4 ± 6.2^{a}	72.7 ± 5.9^{a}	86.0 ± 2.2^{a}	87.2 ± 4.8^{a}
		NG - B	35.1 ± 7.1^{a}	72.0 ± 5.0^{a}	76.7 ± 8.5^{a}	80.7 ± 3.2^{a}
		NG - NB	47.4 ± 5.2^{a}	65.8 ± 4.6^{a}	75.1 ± 3.1^{a}	70.5 ± 8.0^{a}
	Mass of soil recovered (%)	G - B	60.0 ± 3.6^{a}	75.5 ± 3.7^{a}	84.0 ± 4.2^{a}	94.1 ± 1.8^{a}
		G - NB	54.1 ± 2.7^{a}	71.4 ± 3.6^{a}	89.3 ± 1.9^{a}	92.1 ± 2.8^{a}
		NG - B	53.7 ± 8.3^{a}	76.9 ± 3.8^{a}	82.7 ± 3.3^{a}	93.1 ± 0.9^{a}
		NG - NB	57.1 ± 1.6^{a}	72.5 ± 2.3^{a}	79.6 ± 2.6^{a}	84.9 ± 2.9^{a}

Table 1.3 Mean mass recovery (%) and contribution to bulk C (%) in density soil C fractions in burnt and grazed montane grasslands for each depth (0-5, 5-10, 10-20, 20-30 cm) at Wayqecha and Acjanaco.

Fraction	Site		Land use	0-5 cm	5-10 cm	10-20 cm	20-30 cm
LF	Wayqecha (2003)	Fraction of total C (%)	G - B	20.9 ± 8.2^{b}	3.9 ± 1.8^{a}	1.6 ± 0.6^{b}	6.9 ^{a}
			G - NB	64.3 ± 4.0^{a}	25.9 ± 14.4^{a}	3.6 ± 0.1^{b}	3.7^{a}
			NG - B	47.8 ± 9.7^{a}	18.0 ± 9.4^{a}	NA	7.4^{a}
			NG - NB	45.7 ± 5.5^{a}	18.0 ± 9.5^{a}	19.5 ± 8.3^{a}	34.2 ± 19.8^{a}
		Mass of soil recovered (%)	G - B	18.3 ± 7.8^{b}	6.0 ± 3.5^{a}	1.4 ± 0.9^{a}	0.7 ± 0.3^{b}
			G - NB	42.8 ± 7.9^{a}	14.9 ± 5.4^{a}	2.7 ± 2.6^{a}	2.0 ± 1.4^{b}
			NG - B	48.3 ± 6.0^{a}	14.0 ± 5.1^{a}	4.2 ± 3.4 ^{a}	1.3 ± 1.7^{b}
			NG - NB	35.9 ± 3.5^{a}	17.8 ± 5.3^{a}	8.2 ± 3.2^{a}	6.6 ± 0.1^{a}
	Acjanaco (2005)	Fraction of total C (%)	G - B	37.7 ± 3.6^{a}	17.8 ± 2.7^{a}	12.9 ± 1.0^{a}	12.3^{a}
			G - NB	56.8 ± 21.1^{a}	22.9 ± 17.2^{a}	4.3 ± 0.6^{a}	1.3 ± 1.1^{b}
			NG - B	38.9 ± 16.8^{a}	18.1 ± 17.2^{a}	11.0 ± 13.3^{a}	5.1^{ab}
			NG - NB	47.7 ± 17.6^{a}	28.1 ± 12.9^{a}	21.0 ± 8.9^{a}	14.1 ± 1.3^{a}
		Mass of soil recovered (%)	G - B	20.2 ± 7.7^{a}	16.5 ± 2.5^{ab}	10.9 ± 1.1^{a}	8.8^{ab}
			G - NB	30.9 ± 5.3^{a}	31.5 ± 8.9^{a}	3.8 ± 2.1^{a}	1.0 ± 0.1^{b}
			NG - B	31.2 ± 10.6^{a}	12.1 ± 10.0^{b}	7.9 ± 9.5^{a}	2.6^{ab}
			NG - NB	34.9 ± 2.5^{a}	19.9 ± 3.5^{ab}	17.2 ± 4.9^{a}	15.6 ± 3.8^{a}
OLF	Wayqecha (2003)	Fraction of total C (%)	G - B	11.4 ± 9.4^{a}	3.5 ± 2.1^{b}	3.6 ± 0.6^{a}	6.9 ± 6.1a
			G - NB	16.5 ± 8.2^{a}	4.0 ± 2.5^{b}	12.0 ± 9.2^{a}	10.3 ± 10.5^{a}
			NG - B	29.6 ± 3.5^{a}	15.5 ± 3.2^{a}	4.1 ± 2.9^{a}	17.4^{a}
			NG - NB	5.7 ± 4.1^{a}	3.8 ± 1.5^{b}	NA	3.6 ± 2.9^{a}
		Mass of soil recovered (%)	G - B	16.6 ± 6.0^{ab}	5.4 ± 0.4^{b}	3.5 ± 3.7^{b}	1.3 ± 1.1^{a}
			G - NB	11.7 ± 4.9^{ab}	3.7 ± 2.8^{b}	3.4 ± 0.9^{b}	4.0 ± 4.4^{a}
			NG - B	19.1 ± 4.4^{a}	17.8 ± 4.8^{a}	11.8 ± 2.8^{a}	0.9 ± 0.9^{a}
			NG - NB	5.1 ± 3.4^{b}	3.4 ± 1.0^{b}	1.1 ± 3.6^{ab}	0.5 ± 0.2^{a}
	Acjanaco (2005)	Fraction of total C (%)	G - B	24.7 ± 7.1^{a}	11.7 ± 3.4^{a}	20.5 ± 8.1^{a}	4.4^{a}
			G - NB	10.3 ± 4.6^{ab}	1.6 ± 0.3^{b}	8.5 ± 1.2^{a}	9.7^{a}
			NG - B	23.5 ± 9.5^{a}	4.3 ± 3.6^{ab}	12.3 ± 8.0^{a}	8.7^{a}
			NG - NB	6.1 ± 2.4^{b}	10.5 ± 3.8^{a}	4.7 ± 2.0^{a}	3.1 ± 0.5^{a}
		Mass of soil recovered (%)	G - B	19.8 ± 4.2^{ab}	15.0 ± 1.4^{a}	14.7 ± 1.7^{a}	2.8^{a}
			G - NB	8.6 ± 5.9^{b}	3.2 ± 1.4^{c}	3.1 ± 1.6^{b}	5.2^{a}
			NG - B	28.5 ± 12.5^{a}	3.2 ± 2.7^{c}	7.5 ± 2.6^{b}	2.2^{a}
			NG - NB1	4.9 ± 0.7^{b}	8.0 ± 1.2^{b}	4.2 ± 3.0^{b}	4.1 ± 1.1^{a}
HF	Wayqecha (2003)	Fraction of total C (%)	G - B	67.7 ± 4.8^{a}	92.5 ± 0.4^{a}	94.9 ± 0.5^{a}	86.2 ± 13.2^{a}
			G - NB	19.2 ± 12.2^{c}	70.1 ± 14.5^{a}	84.8 ± 9.1a	86.0 ± 13.0^{a}
			NG - B	32.6 ± 6.4^{bc}	66.5 ± 9.2^{a}	NA	75.2^{a}
			NG - NB	48.6 ± 3.7^{b}	70.3 ± 3.4^{a}	76.4 ± 11.3^{a}	62.3 ± 22.5^{a}
		Mass of soil recovered (%)	G - B	62.9 ± 9.4^{a}	83.7 ± 1.8^{a}	92.9 ± 4.6^{a}	96.1 ± 1.7^{a}
			G - NB	49.6 ± 7.0^{ab}	78.0 ± 2.4^{ab}	87.6 ± 5.8^{a}	93.4 ± 6.0^{a}
			NG - B	41.5 ± 4.2^{b}	70.0 ± 6.1^{b}	82.6 ± 3.0^{a}	93.7 ± 2.1^{a}
			NG - NB	57.7 ± 6.7^{ab}	75.7 ± 5.6^{ab}	83.9 ± 5.8^{a}	90.9 ± 2.3^{a}
	Acjanaco (2005)	Fraction of total C (%)	G - B	37.5 ± 8.3^{a}	70.5 ± 5.2^{a}	61.5^{a}	89.0^{a}
			G - NB	32.9 ± 16.3^{a}	75.5 ± 17.2^{a}	87.2 ± 1.7^{a}	89.0 ± 14.2^{a}
			NG - B	37.6 ± 26.3^{a}	77.6 ± 14.2^{a}	76.7 ± 20.9^{a}	86.2^{a}
			NG - NB	46.2 ± 19.9^{a}	61.4 ± 15.7^{a}	74.3 ± 6.9^{a}	82.9 ± 0.7^{a}
		Mass of soil recovered (%)	G - B	57.0 ± 9.1^{a}	67.3 ± 1.5^{b}	75.1 ± 1.6^{a}	87.9^{a}
			G - NB	58.5 ± 0.3^{a}	64.8 ± 7.8^{b}	91.8 ± 82.8^{a}	90.2 ± 9.9^{a}
			NG - B	65.8 ± 23.9^{a}	83.8 ± 6.3^{a}	82.8 ± 12.4^{a}	91.1^{a}
			NG - NB	56.5 ± 2.2^{a}	69.2 ± 4.1^{b}	75.3 ± 3.5^{a}	78.9 ± 3.5^{a}

Table 1.4 Mean sand, silt and clay (%) among the different land uses in the premontane forests.

Depth (cm)	Land use	Sand	Silt	Clay	pH	Bulk density (g cm^{-3})
0-5	VC - F (mature forest)	60 ± 1^{b}	36 ± 6^{c}	4 ± 6^{ab}	5.1 ± 0.2	0.99 ± 0.01
	VC - SL (logged)	74 ± 0^{a}	24 ± 2^{d}	2 ± 2^{c}	5.4 ± 0.1	1.06 ± 0.02
	VC - SF (secondary)	31 ± 1^{d}	64 ± 9^{a}	5 ± 10^{a}	5.5 ± 0.4	0.92 ± 0.02
	VC - AB (abandoned banana)	46 ± 10^{c}	51 ± 9^{b}	3 ± 1^{bc}	5.7 ± 0.3	1.05 ± 0.02
	VC - B (banana)	24 ± 0^{d}	71 ± 1^{a}	4 ± 1^{a}	5.6 ± 0.6	0.92 ± 0.02
	VC - PA (pineapple)	NA	NA	NA	NA	NA
	VC - P (low intensity)	62 ± 0^{b}	36 ± 5^{c}	3 ± 5^{c}	5.6 ± 0.1	1.01 ± 0.01
	VC - P1 (high intensity)	NA	NA	NA	NA	NA
	VC - P2 (abandoned)	NA	NA	NA	NA	NA
5-10	VC - F	44 ± 1^{b}	49 ± 5^{bc}	7 ± 5^{a}	4.9 ± 0.1	
	VC - SL	55 ± 1^{ab}	41 ± 10^{cd}	4 ± 11^{bc}	5.2 ± 0.2	
	VC - SF	21 ± 1^{c}	73 ± 7^{a}	6 ± 7^{a}	5.3 ± 0.1	
	VC - AB	44 ± 12^{b}	53 ± 11^{b}	3 ± 1^{bc}	5.7 ± 0.3	
	VC - B	25 ± 0^{c}	70 ± 3^{a}	5 ± 3^{b}	5.3 ± 0.4	
	VC - PA	NA	NA	NA	NA	
	VC - P	62 ± 0^{a}	35 ± 3^{d}	3 ± 3^{c}	5.6 ± 0.1	
	VC - P1	NA	NA	NA	NA	
	VC - P2	NA	NA	NA	NA	
10-20	VC - F	40 ± 2^{c}	52 ± 7^{b}	9 ± 9^{a}	5.2 ± 0.3	
	VC - SL	55 ± 0^{ab}	41 ± 3^{c}	4 ± 3^{cd}	5.3 ± 0.1	
	VC - SF	20 ± 1^{d}	74 ± 9^{a}	6 ± 9^{b}	5.5 ± 0.1	
	VC - AB	39 ± 1^{c}	57 ± 10^{b}	4 ± 1^{cd}	5.3 ± 0.2	
	VC - B	44 ± 1^{bc}	51 ± 7^{b}	5 ± 8^{bc}	5.2 ± 0.6	
	VC - PA	NA	NA	NA	NA	
	VC - P	63 ± 0^{a}	35 ± 4^{c}	3 ± 4^{d}	5.6 ± 0.1	
	VC - P1	NA	NA	NA	NA	
	VC - P2	NA	NA	NA	NA	
20-30	VC - F	35 ± 3^{c}	53 ± 7^{b}	12 ± 1^{a}	5.2 ± 0	
	VC - SL	73 ± 0^{a}	24 ± 3^{c}	3 ± 3^{c}	5.5 ± 0.1	
	VC - SF	17 ± 1^{d}	76 ± 9^{a}	8 ± 9^{b}	5.6 ± 0.0	
	VC - AB	39 ± 9^{bc}	58 ± 8^{b}	3 ± 0^{c}	5.5 ± 0.1	
	VC - B	49 ± 1^{b}	47 ± 1^{b}	4 ± 8^{c}	5.6 ± 0.5	
	VC - PA	NA	NA	NA	NA	
	VC - P	70 ± 0^{a}	28 ± 9^{c}	2 ± 9^{c}	5.7 ± 0.1	
	VC - P1	NA	NA	NA	NA	
	VC - P2	NA	NA	NA	NA	
0-30	VC - F	45 ± 1^{b}	47 ± 8^{d}	8 ± 3^{a}	NA	
	VC - SL	64 ± 1^{a}	32 ± 9^{e}	3 ± 1^{d}	NA	
	VC - SF	22 ± 6^{d}	71 ± 5^{a}	6 ± 1^{b}	NA	
	VC - AB	42 ± 3^{b}	55 ± 3^{c}	3 ± 0^{cd}	NA	
	VC - B	36 ± 1^{c}	60 ± 1^{b}	4 ± 0^{c}	NA	
	VC - PA	NA	NA	NA	NA	
	VC - P	64 ± 4^{a}	33 ± 3^{e}	2 ± 0^{d}	NA	
	VC - P1	NA	NA	NA	NA	
	VC - P2	NA	NA	NA	NA	

Table 1.5 Mean mass recovery (%) and contribution to bulk C (%) in density soil C fractions among the different land use at the premontane elevation for each depth (0-5, 5-10, 10-20, 20-30 cm).

Fraction		Land use	0-5 cm	5-10 cm	10-20 cm	20-30 cm
LF	Fraction of total C (%)	VC - F (mature forest)	18.5 ± 2.4^{abc}	14.3 ± 1.2^{a}	7.6 ± 1.4^{ab}	12.7 ± 1.6^{ab}
		VC - SL (logged)	28.7 ± 4.4^{a}	5.9 ± 1.1^{c}	5.3 ± 1.8^{ab}	10.8 ± 1.3^{abc}
		VC - SF (secondary)	15.1 ± 2.3^{bcd}	4.0 ± 0.9^{c}	9.0 ± 3.9^{ab}	10.4 ± 2.0^{abc}
		VC - AB (abandoned banana)	21.8 ± 3.1^{ab}	11.7 ± 2.2^{ab}	17.0 ± 1.7^{a}	15.7 ± 4.7^{a}
		VC - B (banana)	17.4 ± 1.4^{abc}	8.2 ± 1.7^{bc}	12.3 ± 6.3^{ab}	11.2 ± 2.2^{abc}
		VC - PA (pineapple)	2.8 ± 0.4^{d}	2.7 ± 1.5^{c}	2 .5 ± 0.9^{ab}	2.7 ± 0.9^{c}
		VC - P (low intensity)	8.5 ± 1.2^{cd}	6.9 ± 0.4^{bc}	6.9 ± 1.8^{ab}	6.8 ± 0.9^{bc}
		VC - P1 (high intensity)	8.7 ± 0.8^{bcd}	10.0 ± 2.0^{abc}	17.0 ± 2.8^{b}	9.8 ±2.5^{abc}
		VC - P2 (abandoned)	10.5 ± 0.5^{bcd}	5.9 ± 2.0^{bc}	5.3 ± 1.0^{ab}	6.0 ±1.5^{bc}
	Mass of soil recovered (%)	VC - F	2.7 ± 0.2^{abc}	2.1 ± 0.3^{a}	1.2 ± 0.1^{a}	0.8 ± 0.1^{a}
		VC - SL	3.7 ± 0.7^{a}	0.4 ± 0.1^{bc}	0.4 ± 0.1^{a}	0.3 ± 0.2^{b}
		VC - SF	2.2 ± 0.4^{abc}	0.3 ± 0.1^{c}	0.4 ± 0.1^{a}	0.8 ± 0.1^{a}
		VC - AB	3.3 ± 0.4^{ab}	1.2 ± 0.1^{ab}	1.2 ± 0.1^{a}	0.4 ± 0.1^{b}
		VC - B	2.5 ± 0.3^{abc}	0.7 ± 0.1^{bc}	1.3 ± 1.1^{a}	0.3 ± 0.1^{b}
		VC - PA	0.6 ± 0.1^{c}	0.8 ± 0.6^{abc}	1.1 ± 0.1^{a}	0.2 ± 0.1^{b}
		VC - P	1.4 ± 0.2^{bc}	1.1 ± 0.1^{abc}	0.6 ± 0.1^{a}	0.3 ± 0.1^{b}
		VC - P1	2.1 ± 0.2^{abc}	2.3 ± 0.1^{a}	1.0 ± 0.1^{a}	0.4 ± 0.1^{b}
		VC - P2	1.5 ± 0.3^{abc}	0.9 ± 0.1^{abc}	0.5 ± 0.1^{a}	0.2 ± 0.1^{b}
OLF	Fraction of total C (%)	VC - F	20.8 ± 2.3^{a}	9.9 ± 0.7^{bc}	6.9 ± 1.3^{b}	12.1 ± 2.6^{bc}
		VC - SL	23.3 ± 4.7^{a}	18.2 ± 2.6^{abc}	7.0 ± 2.2^{b}	3.7 ± 0.6^{bc}
		VC - SF	19.7 ± 2.4^{a}	11.5 ± 2.1^{bc}	12.8 ± 4.7^{b}	10.1 ± 2.0^{bc}
		VC - AB	23.4 ± 2.5^{a}	20.1 ± 4.1^{ab}	20.4 ± 3.7^{ab}	12.7 ± 3.5^{ab}
		VC - B	17.2 ± 4.0^{a}	22.9 ± 2.8^{a}	26.8 ± 6.9^{a}	24.7 ± 5.8^{a}
		VC - PA	8.2 ± 1.2^{a}	6.7 ± 0.2^{c}	8.7 ± 2.0^{b}	8.6 ± 4.0^{c}
		VC - P	13.8 ± 0.7^{a}	12.5 ± 1.0^{bc}	10.1 ± 2.4^{b}	12.0 ± 2.2^{bc}
		VC - P1	14.0 ± 1.4^{a}	15.2 ± 2.5^{abc}	10.0 ± 1.4^{b}	11.7± 2.0^{bc}
		VC - P2	16.0 ± 2.0^{a}	8.9 ± 0.8^{bc}	9.3 ± 2.0^{b}	10.7± 0.5^{bc}
	Mass of soil recovered (%)	VC - F	4.9 ± 0.6^{a}	2.3 ± 0.1^{b}	1.4 ± 0.2^{a}	2.1 ± 0.4^{b}
		VC - SL	3.3 ± 0.3^{ab}	1.4 ± 0.1^{bc}	0.7 ± 0.1^{a}	0.4 ± 0.1^{b}
		VC - SF	2.1 ± 0.3^{b}	0.6 ± 0.1^{c}	0.5 ± 0.1^{a}	0.6 ± 0.2^{b}
		VC - AB	4.2 ± 1.3^{ab}	1.8 ± 0.3^{b}	1.4 ± 0.2^{a}	1.0 ± 0.2^{b}
		VC - B	1.8 ± 0.2^{b}	1.4 ± 0.3^{bc}	1.6 ± 0.7^{a}	4.1 ± 0.6^{a}
		VC - PA	2.9 ± 0.7^{ab}	1.8 ± 0.2^{bc}	1.5 ± 0.1^{a}	1.5 ± 0.2^{b}
		VC - P	1.6 ± 0.2^{b}	1.4 ± 0.2^{bc}	0.8 ± 0.3^{a}	0.5 ± 0.1^{b}
		VC - P1	3.5 ± 0.2^{ab}	2.7 ± 0.1^{a}	2.1± 0.1^{a}	2.4± 0.2^{b}
		VC - P2	2.2 ± 0.4^{ab}	1.6 ± 0.2^{bc}	2.5± 0.1^{a}	1.3± 0.2^{b}
HF	Fraction of total C (%)	VC - F	60.7 ± 3.6^{cd}	75.8 ± 1.4^{ab}	85.5 ± 1.7^{ab}	75.3 ± 5.2^{ab}
		VC - SL	48.0 ± 5.3^{d}	75.9 ± 3.3^{ab}	87.7 ± 3.8^{a}	76.1 ± 3.5^{ab}
		VC - SF	65.2 ± 4.2^{bc}	84.5 ± 2.9^{a}	78.2 ± 8.4^{ab}	75.9 ± 4.4^{ab}
		VC - AB	54.8 ± 3.1^{cd}	68.2 ± 5.0^{b}	62.6 ± 2.1^{ab}	65.2 ± 2.1^{b}
		VC - B	65.5 ± 3.0^{bc}	68.8 ± 2.8^{b}	60.9 ± 6.9^{ab}	64.1 ± 6.2^{b}
		VC - PA	89.0 ± 1.0^{a}	90.7 ± 1.4^{a}	88.7 ± 1.5^{a}	88.7 ±1.1^{a}
		VC - P	77.7 ± 1.1^{ab}	80.6 ± 1.3^{ab}	77.2 ± 10.0^{ab}	79.8 ± 9.2^{a}
		VC - P1	76.0 ± 3.5^{abc}	72.0 ± 1.5^{ab}	72.5 ± 2.2^{ab}	77.0 ± 5.0^{ab}
		VC - P2	71.0 ± 5.0^{abc}	85.2 ± 3.1^{ab}	85.5 ± 3.0^{ab}	82.1 ± 2.4^{a}
	Mass of soil recovered (%)	VC - F	99.3 ± 0.8^{a}	99.0 ± 1.3^{ab}	98.3 ± 1.1^{a}	100.5 ± 0.9^{ab}
		VC - SL	98.4 ± 1.5^{a}	98.9 ± 1.2^{a}	99.0 ± 1.5^{ab}	101.5 ± 0.9^{a}
		VC - SF	97.5 ± 0.8^{a}	97.3 ± 0.7^{ab}	99.3 ± 0.9^{ab}	99.2 ± 1.6^{ab}
		VC - AB	98.2 ± 1.3^{a}	97.6 ± 0.8^{ab}	97.8 ± 0.6^{ab}	97.6 ± 0.2^{ab}
		VC - B	97.6 ± 1.4^{a}	95.7 ± 0.5^{b}	99.6 ± 1.5^{ab}	98.6 ± 1.6^{ab}
		VC - PA	97.0 ± 1.1^{a}	99.7 ± 0.7^{ab}	97.7 ± 3.1^{ab}	96.3 ± 0.6^{ab}
		VC - P	96.0 ± 0.4^{a}	96.5 ± 0.8^{ab}	96.8 ± 1.3^{b}	96.9 ± 1.2^{ab}
		VC - P1	92.4 ± 1.2^{a}	95.5 ± 0.6^{b}	99.6 ± 1.3^{b}	92.4 ± 1.2^{ab}
		VC - P2	95.6 ± 1.0^{a}	98.6 ± 1.0^{ab}	99.6 ± 1.3^{b}	102.3 ± 1.2^{ab}
Total C (Mg C ha^{-1})		VC - F (mature forest)	7.3 ± 2.6^{a}	6.0 ± 1.4^{a}	8.7 ± 1.2^{ab}	6.4 ± 1.9^{abc}
		VC - SL (logged)	6.6 ± 2.8^{a}	4.7 ± 1.1^{a}	6.9 ± 1.4^{bc}	5.3 ± 1.5^{abc}
		VC - SF (secondary)	6.7 ± 1.2^{a}	3.2 ± 0.6^{a}	6.9 ± 1.4^{c}	7.5 ± 2.5^{ab}
		VC - AB (abandoned banana)	6.4 ± 3.0^{a}	3.9 ± 2.1^{a}	5.8 ± 1.2^{c}	4.4 ± 2.1^{bc}
		VC - B (banana)	4.6 ± 1.3^{a}	3.6± 0.6^{a}	5.4 ± 0.5^{c}	2.7 ± 0.5^{c}
		VC - PA (pineapple)	9.8 ± 2.3^{a}	6.6 ± 0.8^{a}	10.4 ± 0.2^{a}	7.1± 1.2^{ab}
		VC - P (low intensity)	4.8 ± 1.8^{a}	3.8 ± 1.8^{a}	6.7 ± 0.5^{bc}	3.7 ± 2.9^{c}
		VC - P1 (high intensity)	9.1 ± 1.3^{a}	5.4 ± 1.5^{a}	7.8 ± 0.2^{abc}	6.1 ± 2.9^{abc}
		VC - P2 (abandoned)	10.7 ± 0.3^{a}	5.6 ± 0.6^{a}	9.8 ± 1.3^{a}	10.1 ± 2.9^{a}

2.1 Appendix for chapter 3

Table 2.1 Significant relationships between soil CO_2 flux and the environmental data for two burnt and non burnt montane grassland sites and grazed subplots. Significant code * = P< 0.05

Site and burn year	Land use	Variable	Chi squared	Degrees of freedom	P-value	Intercept	Slope
	ALL DATA	Air temperature	10.92	1	0.0001 *	-0.51 ± 0.10	0.00 ± 0.00
		Soil temperature	24.07	1	9.3×10^{-7} *		0.03 ± 0.01
		Season	4.6	1	0.031 *		-0.04 ± 0.02
2003	Burnt – grazed	-	-	-	-		-
(Wayqecha)	Non burnt – grazed	Air temperature	5.97	1	0.01 *	-0.34 ± 0.11	0.01 ± 0.00
	Grazed - non burnt	Air temperature	10.26	1	0.001 *	0.01 ± 0.09	0.00 ± 0.00
	Non grazed – non burnt	Soil temperature	9.34	1	0.002 *	-0.30 ± 0.22	0.01 ± 0.01
		Air temperature	5.09	1	0.024 *		0.00 ± 0.00
		Season	8.31	1	0.004 *		0.10 ± 0.03
2005	Burnt – grazed	-	-	-	-		-
(Acjanaco)	Non burnt – grazed	Air temperature	17.30	1	3.2×10^{-5}	0.04 ± 0.10	-0.010 ± 0.02
	Grazed - non burnt	Soil temperature	19.43	1	1.0×10^{-5} *	-0.01 ± 0.12	-0.006 ± 0.01
	Non grazed – non burnt	Air temperature	6.94	1	0.008 *	-0.40 ± 0.10	0.014 ± 0.01

Table 2.2 Significant relationships between soil CO_2 flux and the environmental data for burnt and non-burnt montane cloud forest sites. Significant code * = P< 0.05

Site and burn year	Site	Variable	Chi squared	Degrees of freedom	P-value	Intercept	Slope
2003	Burnt	Air temperature	9.89		0.002 *	-0.151 ± 0.118	0.020 ± 0.007
(Wayqecha)	Non burnt	-	-	-	-	-	-
2005	Burnt	-	-	-	-	-	-
(Acjanaco)	Non burnt	-	-	-	-	-	-
2010	Burnt	-	-	-	-	-	-
(Sunchubamba)	Non burnt	-	-	-	-	-	
All sites	BURNING	Soil temperature	5.26	1	0.02 *	-0.551 ± 0.125	0.018 ± 0.008
combined		Air temperature	4.17	1	0.04 *		0.006 ± 0.003
		Month	25.13	1	5.4×10^{-07} *		0.185 ± 0.035
		Month ^ 2	19.49	1	1.0×10^{-05} *		-0.021 ± 0.005
All sites	ALL DATA	Air temperature	230.83	1	2.2×10^{-16} *	-0.317 ± 0.06	0.009 ± 0.003
combined		Month	37.00	1	1.1×10^{-9} *		0.168 ± 0.027
		Month ^ 2	28.20	1	1.1×10^{-7} *		-0.019 ± 0.003

Table 2.3 Significant relationships between soil CO_2 flux and the environmental data for the different land uses in the premontane elevation. Significant code * = P< 0.05

Site	Variable	Chi squared	Degrees of freedom	P-value	Intercept	Slope
ALL DATA	VWC	8.78	1	0.003*	0.687 ± 0.143	-0.008 ± 0.002
	Month	16.97	1	3.8×10^{-5} *		0.121 ± 0.029
	Month ^ 2	21.41	1	3.7×10^{-6} *		-0.016 ± 0.003
	Site	27.41	5	4.7×10^{-5} *		-0.041 ± 0.071
VC - MF	VWC	3.70	1	0.054*	1.296 ± 0.396	-0.020 ± 0.008
VC - SL	Air temperature	7.82	1	0.005 *	0.530 ± 0.353	-0.004 ± 0.014
VC - SF	Soil temperature	5.87	1	0.015 *	-1.034 ± 0.392	0.059 ± 0.017
VC - AB	VWC	11.18	1	0.0008 *	1.430 ± 0.268	-0.021 ± 0.006
VC - B	-	-	-	-		
VC - P	Air temperature	7.17	1	0.007 *	0.541 ± 0.165	-0.010 ± 0.005
	Month	14.23	1	0.0001 *		0.282 ± 0.070
	Month ^ 2	14.74	1	0.0001 *		-0.033 ± 0.008

Table 2.4 Relationship between CO_2 fluxes and decomposition rates on burnt and grazed plots in montane grasslands

Land use	Slope	Intercept	R^2
Wayqecha	0.0592	1.5581	0.0672
Acjanaco	-0.1751	0.3848	0.9911
Grazing	-0.1857	0.4519	0.2838
Burning	-0.0598	0.9	0.0765
ALL SITES	-0.0811	0.7262	0.1703

Table 2.5 Decomposition rates for burnt and non-burnt plots in montane grasslands

Site	Land use	Slope	Intercept	R^2
Wayqecha	grazed – burnt	-0.05	101.75	0.71
	grazed – non burnt	-0.19	101.98	0.77
	non grazed – burnt	-0.12	104.02	0.87
	non grazed – non burnt	-0.07	98.78	0.74
Acjanaco	grazed – burnt	-0.03	99.33	0.39
	grazed – non burnt	-0.04	99.03	0.64
	non grazed – burnt	-0.04	99.13	0.59
	non grazed – non burnt	-0.04	99.29	0.62
	Grazing	-4.23	104.53	0.98
	Non grazing	-3.11	103.63	0.94
	Non burning	-3.76	104.82	0.97
	Burning	-3.57	103.34	0.96

Table 2.6 Decomposition rates for burnt and non-burnt plots in montane cloud forests

Site	Land use	Slope	Intercept	R^2
Wayqecha	burnt	-5.68	109.20	0.77
	non burnt	-6.59	110.40	0.73
Acjanaco	burnt	-4.71	105.89	0.98
	non burnt	-5.46	108.27	0.93
Sunchubamba	burnt	-8.53	113.09	0.93
	non burnt	-5.89	109.27	0.89
	BURNING	-6.31	109.39	0.92
	NON BURNING	-5.98	109.31	0.88

3.1 Appendix for chapter 4

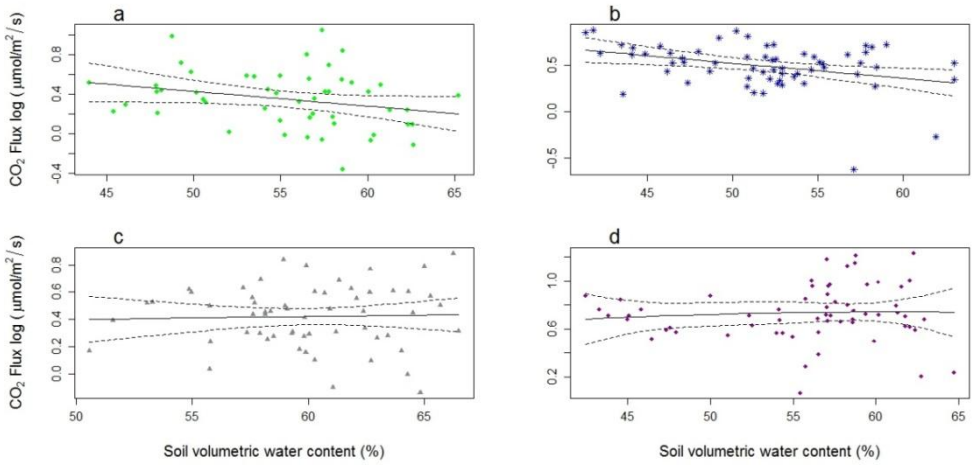


Figure 3.1 Linear relationships between logged soil CO_2 flux (µmol/ m^2/s) and VWC from the field experiment that took place in 2013, where CO_2 flux measurements were carried out on 5 collars, morning and afternoon every two months for a year on all four sites (a) mature forest; b) cultivated banana; c) abandoned banana; d) pasture). The lines represent the linear regression and dashed lines represent 95 % confidence limits for the data.

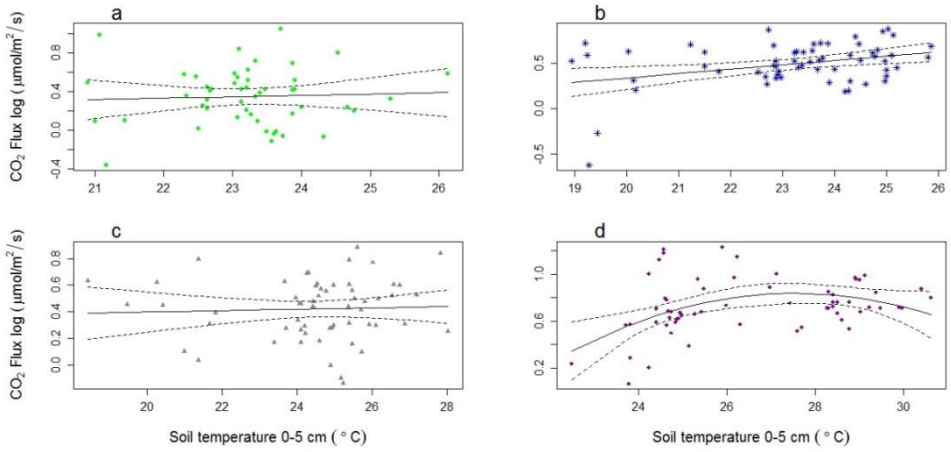


Figure 3.2 Linear relationships between logged soil CO_2 flux (µmol/m^2/s) and soil temperature from the field experiment that took place in 2012, where CO_2 flux measurements were carried out on 5 collars, morning and afternoon every two months for a year on all four sites (a) mature forest; b) cultivated banana; c) abandoned banana; d) pasture). The lines represent the linear regression and dashed lines represent 95 % confidence limits for the data.

Table 3.1 Relationship between annual soil CO_2 flux with soil VWC, soil temperature (0-5 cm) and air temperature for the four different land uses.

Relationship	Site	Slope	Intercept	c	R^2	P-value
Soil volumetric water content	VC-F	- 0.019	1.169		0.070	0.05*
	VC-B	0.002	0.298		0.119	0.82
	VC-AB	- 0.016	1.342		0.001	0.01*
	VC-P	0.003	0.585		0.004	0.62
Soil temperature	VC-F	0.014	0.017	-	0.003	0.73
	VC-B	0.005	0.296	-	0.002	0.74
	VC-AB	0.048	- 0.629	-	0.120	0.01*
	VC-P (polynomial)	1.054	- 13.68	- 0.019	0.162	0.01*
Air temperature	VC-F	0.001	0.710		0.006	0.59
	VC-B	0.011	0.106		0.029	0.20
	VC-AB	0.019	0.020		0.071	0.04*
	VC-P	0.011	0.052		0.000	0.90

Field experiment took place in 2012 where CO_2 flux measurements were carried out on 5 collars, morning and afternoon every two months for a year on all four sites (refer to chapter 3 for full methods and results).

Table 3.2 CO_2 flux means (umol/m^2/s) with standard deviations for the each temperature and linear relationships between soil CO_2 flux with temperature (ranging from 16 – 32 °C) on the four different soils.

Site	CO_2 flux at 16 °C	CO_2 flux at 24 °C	CO_2 flux at 28 °C	CO_2 flux at 32 °C	Slope	Intercept	R^2	P-value	Degrees of freedom
VC-AB	0.2 ± 0.2^{gh}	0.3 ± 0.2^{efgh}	0.5 ± 0.3^{abcd}	0.6 ± 0.2^{ab}	0.03	-1.342	0.38	4.1×10^{-10} *	82
VC-B	0.2 ± 0.1^{h}	0.4 ± 0.2^{cdef}	0.5 ± 0.2^{abcd}	0.7 ± 0.3^{a}	0.04	-1.452	0.60	2.2×10^{-16} *	81
VC-F	0.2 ± 0.1^{h}	0.3 ± 0.2^{defg}	0.6 ± 0.3^{abc}	0.6 ± 0.3^{ab}	0.04	-1.360	0.53	1.2×10^{-14} *	81
VC-P	0.2 ± 0.1^{fgh}	0.4 ± 0.2^{bcde}	0.5 ± 0.2^{abcd}	0.9 ± 0.5^{a}	0.03	-1.221	0.49	1.3×10^{-13} *	80

Significant codes: * 0.05. Simple linear regression lm(Flux~Temperature) for each site with moisture combined.

Table 3.3 CO_2 flux means (umol/m^2/s) with standard deviations for the each moisture band and linear relationships between soil CO_2 flux with VWC (ranging from 25 – 60%) on the four different soils

Site	CO_2 flux at 25% VWC	CO_2 flux at 40% VWC	CO_2 flux at 60 % VWC	Slope	Intercept	R^2	P-value	F statistic	Degrees of freedom
VC-AB	0.29 ± 0.20^{b}	0.47 ± 0.28^{ab}	0.49 ± 0.31^{ab}	0.006	-0.777	0.083	0.008 *	7.398	82
VC-B	0.34 ± 0.20^{ab}	0.46 ± 0.26^{ab}	0.56 ± 0.41^{a}	0.003	-0.634	0.045	0.054 *	3.826	81
VC-F	0.54 ± 0.03^{a}	0.41 ± 0.25^{ab}	0.32 ± 0.17^{ab}	-0.004	-0.276	0.065	0.021 *	5.53	80
VC-P	0.48 ± 0.24^{a}	0.53 ± 0.26^{a}	0.48 ± 0.52^{ab}	-0.002	-2.849	0.016	0.260	1.286	81

Significant codes: * 0.05. Simple linear regression lm(Flux~ VWC) for individual sites and temperatures combined.

Table 3.4 Mixed model relationships between soil CO_2 flux with soil VWC, temperature and time. Cores with very high VWC from the mature forest were removed. Significant codes: * 0.05

Site	Treatment	Chi squared	P-value	Intercept	Slope
V - F	Temperature: VWC	1.0024	0.35		
	Temperature	65.507	5.8×10^{-16} *	-1.115 ± 0.112	0.037 ± 0.003
	VWC	939227	0.001 *		-0.005 ± 0.001
	Time	0.7061	0.40		
All data	Temperature: VWC	0.0858	0.77		
	Temperature	263.21	2.2×10^{-16} *	-1.350 ± 0.045	0.036 ± 0.002
	VWC	0.5827	0.45		
	Time	2.7657	0.10		
	Site	4.2859	0.23		